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MEGANTHROPUS, AUSTRALOPITHECINES AND HOMINIDS

J. T. ROBINSON
Transvaal Museum, Pretoria, South Africa

SIX FIGURES

"MEGANTHROPUS" AFRICANUS

In the course of his 1939 East African Expedition, Kohl-Larsen discovered a number of fossil remains, including more of the hominid which Weinert has called *Africanthropus.* About 40 km north of the locality of "*Africanthropus*" I, he discovered a fragment of maxilla containing P^3 and P^4. Some distance away (both 6 and 3 km away, according to Weinert, '50) a single, worn, upper molar was found. These have been mentioned and named (Weinert, '50, '51) and described (Remane, '51).

Weinert considered these two specimens to belong to the same type of animal, apparently on the strength of their similar coloring and specific gravity, and named the creature *Meganthropus africanus.* According to Remane ('51) the first mention of this form was by Hennig ('48), a paper which unfortunately is not available to me at present. In this Hennig has listed the specimen as *Präanthropus,* which, as Remane remarks, is not in accordance with the taxonomic rule which demands that each form have a trivial name as well as a generic one. Remane therefore rejects the latter name and accepts that given by Weinert. Weinert, however, gives no cogent reasons for using the generic name *Meganthropus.* He seems to have placed the form in this genus largely because the maxillary fragment agrees, in size, more nearly with the

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Meganthropus II mandible (i.e., the 1941 specimen) from Java than it does with "*Africanthropus*" — from which it also differs in colour and specific gravity (see Weinert, '50, pp. 139–141). He mentions that Broom recovered a mandible of similar size to that of *Meganthropus palaeojavanicus* but gives no comparisons with any australopithecines.

Remane ('51) considered the structure of the teeth in detail and agrees with Weinert in assigning the specimen to the genus *Meganthropus*. He considered the possibility of it be-

TABLE 1

Comparative measurements of upper premolars

	P^3		MODULE	P^4		MODULE
	Length	Breadth		Length	Breadth	
M. africanus (Rem.)	8.6	12.3	10.5	9.1	12.5	10.8
Plesianthropus (Rob.)						
T.M. 1511	9.2	12.3	10.8	9.3	12.8	11.1
Sts. 12	8.9	12.1	10.5	9.3	12.2	10.8
Sts. 17	8.6	13.0	10.8	8.5	13.3	10.9
T.M. 1512	8.7	12.0	10.4	...	...	...
Sts. 1 left	9.5	13.6	11.6	..	...	...
Sts. 1 right	9.4	13.3	11.4	..	...	...
P. crassidens (Rob.)	9.6	13.8	11.7	10.5	15.8	13.2
P. robustus (Rob.)	10.3	13.8	12.1	10.0	15.2	12.6
Pithecanthropus (Weid.)	8.4	12.4	10.4	8.4	12.3	10.4
Sinanthropus (Weid.)	8.3	11.9	10.1	7.9	11.4	9.7
Australian (Campb.)	7.8	10.3	9.1	7.2	10.1	8.7
White (Black)	7.2	9.1	8.2	6.8	8.8	7.8

ing an australopithecine but rejected it. The grounds for doing this but referring it to *Meganthropus* seem to me obscure, but these will be dealt with below.

Remane rightly points out that the dimensions of the teeth are not as important as their morphology in assessing relationships. However, as all possible characters should be employed — with due regard to relative merit — table 1 sets out some relevant comparative measurements, in millimeters.

In the case of *P. crassidens, Sinanthropus* and the two ethnic groups of modern man the values given are mean values and

the modules are modules of the means. In all other cases the values are for single specimens. In the case of *Plesianthropus* separate dimensions are given for each of the known, measurable specimens. This was done, in preference to giving a mean value, because this australopithecine comes nearest to *Meganthropus africanus* in respect to the sizes of P^3 and P^4.

It is at once apparent from these figures that the modules for P^3 and P^4 of *Meganthropus africanus* fall within the ranges of variation for those of *Plesianthropus*, even though

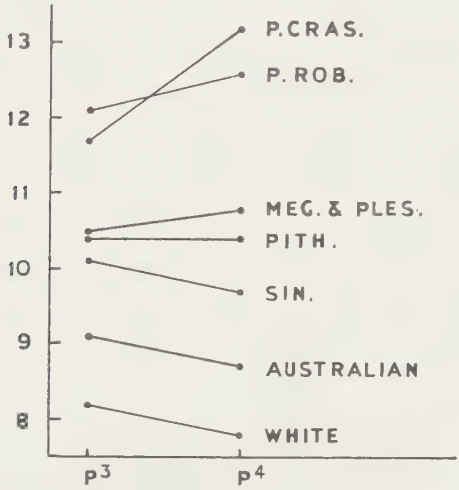

Fig. 1 Comparison of the modules of P^3 and P^4 in a number of hominids.

specimens of these teeth are known from only 5 individuals of the latter. Sts. 12 has teeth of the same size as *M. africanus*. The two species of *Paranthropus* have appreciably larger teeth. *Pithecanthropus, Sinanthropus* and modern man have smaller teeth, though in the case of *Pithecanthropus* the difference is very slight.

A further fact emerging from this table is that in *M. africanus* and the australopithecines P^4 is larger than P^3. In the one *Pithecanthropus* specimen these two teeth are the same size while in *Sinanthropus* and modern man P^4 is smaller than P^3. This latter relation appears to be universal among

true hominids. *Pithecanthropus,* as far as is known, is almost intermediate in having P^3 and P^4 approximately equal in size. The measurements given by Weidenreich show P^4 smaller than P^3 by 0.1 mm in breadth — but this slight degree of difference cannot be considered significant because it would be more than obscured by personal error in measuring. Whether this relation is true for *Pithecanthropus* is therefore not certain.

The size ratio of these two teeth is not without significance because some workers have held that $P^3 > P^4$ is a hominid character and forms not exhibiting it cannot be classified as hominids. However I have elsewhere (Robinson, '52) attempted to show some of the main points in the evolution of size in the hominid dentition and to show that in the general reduction of size, changes in relative size have also occurred. One of these changes in relative size almost certainly involves the relatively more rapid reduction of P^4 compared to P^3. The relationship $P^3 < P^4$ seems to be characteristic of the prehominid stage. It is unfortunately not possible at present to discover whether the latter relationship holds for the true genus *Meganthropus* as the appropriate teeth are not known for *M. palaeojavanicus.*

Remane ('51) concludes, in his study of the morphological features of the *M. africanus* premolars, that they exhibit fairly marked pongid features, while the australopithecines are "ultrahominid" in this respect. On page 322 he gives a table setting out his view of the distinction between the pongid type and the hominid type. He shows that in almost all features *M. africanus* agrees with the pongid type. This is especially shown in the difference in shape in occlusal view, between P^3 and P^4, the complexity of the occlusal surface of P^3, the development of two buccal grooves with fairly marked remains of the buccal cingulum and the possession of three roots. In his opinion only the latter feature is found in australopithecines; in all other features they agree with the hominid type and thus differ from *M. africanus.*

In the small collection of *Plesianthropus* specimens there is only one (Sts. 1) in which P^3 is almost unworn. P^3 is present bilaterally but P^4 is absent. A photograph of this specimen is reproduced as figure 17, plate 4, in Broom, Robinson and Schepers ('50). P^3 from the left side is illustrated here in figure 2. From this it is manifest that the occlusal surface of this tooth is very similar to that of the *M. africanus* tooth, but the former has a more complicated crenulation of the surface. P^3 of Sts. 12, on the other hand, has a similarly shaped occlusal surface which is absolutely smooth except for the simple hominid-type fissure system.

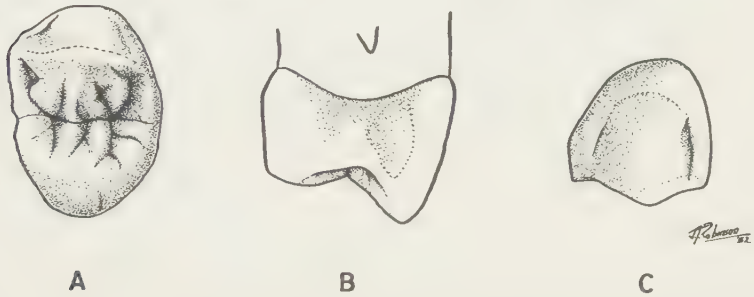

Fig. 2 P^3 in *Plesianthropus*. A. Occlusal view of tooth from left side of Sts. 1. B. Mesial view of tooth from left side of Sts. 12. C. Buccal view of Sts. 49. All × 2.

The buccal face is equally smooth and uncomplicated. In Sts. 1 the buccal face has a well marked mesial buccal groove with a well defined ridge mesial to it. The distal buccal groove is not so clearly defined and the ridge distal to it is also small. In the left P^3 of Sts. 17 the mesial buccal groove and ridge are strongly developed. As far as can be determined P^3 has three portions to the root: two buccal portions and one lingual.

The known P^3 of *M. africanus* therefore comes remarkably close to some of the *Plesianthropus* homologues. The variability in structure and size in *Plesianthropus* would seem to allow the inclusion of the *M. africanus* tooth without difficulty. The two species of *Paranthropus* do not approach the *M. africanus* form closely in either size or structure.

It is worth mentioning here that although Remane considers that the roots of P^3 of the australopithecines approach the pongid form closely, the difference is nevertheless considerable. In *M. africanus, Plesianthropus* and *P. robustus* the known specimens of P^3 appear to have three roots but as all are in situ there can be no certainty on this point. In the case of *P. crassidens* a number of isolated specimens are available in which the roots are intact. There are either two separate roots, a buccal and a lingual one, or there are two buccal ones and a lingual one which is fused to the mesial buccal root. This latter type is the usual form and the fusion is marked; usually only the apices are separate. No cases are known in which the lingual root fuses with the distal buccal one. Remane ('21) has shown that where fusion of the lingual root occurs with one of the buccal ones in the pongids, it is always with the distal buccal one. He found no instance of the type of fusion seen in the australopithecines. The above applies also to P^4 in *P. crassidens.* In one specimen (SK 65) in which P^3 and P^4 are in situ but the buccal region of the roots and maxilla is damaged, both the buccal roots appear to be unfused with the lingual one in both P^3 and P^4.

This strongly suggests a very real distinction between the roots of these teeth and those of pongids even where an apparently strong similarity appears to exist. In fact it is difficult to reconcile the structure of the *P. crassidens* roots with the picture of the structure and evolution of those of the pongids as we know them at present.

It is therefore a great pity that the roots of the *M. africanus* teeth are obscured by bone. It would be an important point if the roots proved to be fused in the australopithecine fashion.

In *M. africanus* P^4 differs considerably from P^3. The crown is more symmetrical and the occlusal surface is simpler. The fissure system is essentially hominid and the enamel surface is almost smooth. The buccal face is also less complicated. The buccal grooves are lightly marked and the ridges poorly developed and are only visible for a short distance mesially

and distally; not almost continuous as in P^3. The upward extension of the cervical line is centrally placed; the corresponding extension in P^3 is situated mesialward of the center. These features may also be found among the *Plesianthropus* teeth. P^4 is less variable in structure in the collection of *Plesianthropus* teeth but nevertheless variations do exist. In one case the occlusal surface is rather more square in shape than is the case in *M. africanus* but in the other cases the shape is similar to that in the latter form. The fissure system is simpler than that of P^3 but is not always as simple as that in *M. africanus*. The greater symmetry of the buccal face found in *M. africanus* is also characteristic of *Plesianthropus*. In only one case a little can be seen of the buccal roots of P^3 and P^4 and here there is also a marked similarity to *M. africanus*. That is, two buccal roots are present in both teeth but they are either partly fused or closely approximated in P^4 but not in P^3.

An isolated molar was also found some distance away from the site of discovery of the maxillary fragment. Weinert ('50) says, on page 139, that this specimen was found 6 km away but on page 141 says the distance was 3 km. Whichever is the case it means that the possibility of this specimen belonging to another type is a real one. In the Sterkfontein area the sites of recovery of *P. crassidens* and *Plesianthropus* are separated by less than one mile and yet these two forms differ so markedly in a number of dental and other features that they certainly cannot be placed in the same species and perhaps not even in the same genus. Furthermore the molar is almost featureless through wear and is unlikely to belong to the same individual as the premolars which are lightly worn. If the molar is M^3 as Remane thinks, it certainly could not have belonged to the same individual. This tooth is therefore not considered in this discussion (a) because it is too worn to be of much diagnostic value, and (b) because it is by no means certain, color and specific gravity notwithstanding, that it does belong to *M. africanus*.

From the foregoing it is readily apparent that the characters of *M. africanus* may all, as far as they are at present known, be found among the australopithecines. Not only this, all may be duplicated within a small collection of the relevant elements of a single species of australopithecine, *Plesianthropus transvaalensis*. In view of this fact it seems necessary to reconsider the assessment of the affinities of this specimen by Weinert and Remane. I can find no clear statement of any cogent reasons for referring the specimen to the genus *Meganthropus* in the work of either of these authors. Weinert gives no real comparisons of this specimen with other possibly related forms other than a series of photographs, with brief comments, of it with a cast of *Meganthropus* II from Java. Remane gives a much fuller treatment, including comparison with some australopithecines, but finds lack of identity or close relationship in respect of both size and structure. However, had he had access to the collections of australopithecine material he would doubtless have drawn different conclusions. He remarks, on page 325, that on the grounds of the geographical position and the geological age of the specimen there would appear to be a small degree of relationship between it and the australopithecines but that the morphological facts do not fit this "natural" solution to the question of relationship. He goes on to point out that the teeth of *"Meganthropus" africanus* resemble the pongid type much more than do the australopithecines, which are even closer to the hominid type than *Sinanthropus*. This latter point is undoubtedly true of *P. crassidens* and possibly of some of the other ape-men, but not of *Plesianthropus*. In this form the morphological variability in respect of the upper premolars is sufficiently great to include teeth like those of *M. africanus* as well as more obviously hominid types.

The fact that the specimen was found in East Africa and exhibits such marked similarity to one of the australopithecines from South Africa makes generic identity with the Javanese fossil unlikely. A more serious objection to considering this specimen congeneric with *M. palaeojavanicus*

is the fact that upper premolars of the latter form have never been described and, to my knowledge, are unknown. It is probable that, if known, the premolars of the Javanese form would resemble those of the East and South African forms very strongly, but that is only supposition in the absence of any concrete evidence.

In my opinion *"Meganthropus" africanus* is an australopithecine, which is almost certainly more closely related to the South African forms than to *M. palaeojavanicus*. There seems to be no justification for referring it to the genus *Meganthropus*. If it is to be referred to an already existing genus then *Plesianthropus* is the obvious choice. However the available material is too scanty to allow of certainty in referring it to any known genus. There seem to be no important features about the specimen differentiating it from *Plesianthropus* but this does not mean that additional material would not bring such differences to light. It is quite probable that additional specimens would show that the species should be placed in a new genus, but coining a new generic name at this stage seems to me unwise and, in fact, unjustifiable as the known specimen cannot be satisfactorily distinguished from *Plesianthropus*. It seems wiser to leave the baptism of this type until more specimens are available. The chief importance of the specimen lies in the fact that it proves that the australopithecines were not confined to southern Africa. This is additional support for the proposition that the australopithecines were at one time a widely distributed group.

MEGANTHROPUS PALAEOJAVANICUS AND THE AUSTRALOPITHECINES

The problem of this East African specimen raises more acutely the more general problem of the relationship between the australopithecines and some eastern hominids, especially *Meganthropus*.

Enough specimens broadly related to man are now known to show that two main divisions exist in the hominid group. Heberer has divided the family Hominidae into the subfami-

lies Praehomininae and Euhomininae to express this fact. This usage should not be confused with another which classifies the early euhominids as prehominids. Following Boule ('37), von Koenigswald has used the term Praehominidae for the *Pithecanthropus-Sinanthropus* group. A similar usage is employed by Teilhard de Chardin ('51). The question here arises whether the subfamily name Praehomininae is valid. Heberer ('51b, p. 61) equates it with Australopithecinae, a term which he discards, as he does the generic name *Australopithecus*. However the term Australopithecinae was used as a subfamily name by Gregory and Hellman in 1939 and must therefore take precedence. The family Hominidae must therefore be divided into the subfamilies Australopicinae and Euhomininae; the former includes the South African australopithecines, the East African specimen and, as will appear in the remainder of this paper, also *Meganthropus palaeojavanicus*. The Euhomininae include *Telanthropus, Pithecanthropus, Sinanthropus* and later forms. However the term prehominid is less cumbersome and more euphonious than Australopithecinae and will be retained here as a descriptive term applied to the specimens comprising this subfamily — but Australopithecinae must remain as the correct nomenclatural name for the subfamily. The affinities of *Gigantopithecus* are not clear but possibly it also belongs in the prehominid group. The relationships within the euhominids are enormously complex but three broad groups may be differentiated: (a) the primitive forms which had relatively recently passed from the prehominid grade of organization, e.g. *Pithecanthropus* and *Sinanthropus,* (b) the more advanced forms, e.g. Cro Magnon and living forms, and (c) the neanderthaloid forms which appear to be an extinct group not directly ancestral to modern man.

This classification is brief and purposely rather vague. Very little is known about the nature of the evolutionary processes in the hominids or of the details of their phylogenesis. It is not even certain whether either or both of the

stages (b) and (c) arose from the known specimens comprising (a). These latter forms, (a), may very easily be marginal forms in the hominid evolutionary stream. The older conception of family trees of a branching geometrical nature is passing and in doing so is metamorphosing in the oddest ways, now taking on a reticulate and vaguely Bryozoan shape or blossoming forth replete with ornamental vases, leaves and exotic blooms! The modern concept is more that of a broad stream, in the time dimension, of living forms complexly interrelated. Groups diverge from the central stream for longer or shorter periods so that the interchange of evolutionary material between this group and the main stream is slowed down or temporarily stopped. Such a group may develop into a secondary current within the confines of the main flow, develop into a parallel or divergent streamlet or perhaps merely form diminishing eddies at the margin. The possibilities of relationships within such a space-time structure are very great and a detailed reconstruction of the actual paths taken in the past is a fantastically difficult or even impossible task. What apparent lines of development an individual student sees in the material at present available depends to a very great extent on his particular views on the nature of the evolutionary process and what characters afford good clues to the path taken by any particular specimen. Because of the relative paucity of our knowledge there are extremely divergent and even completely contradictory views on these points. This is perhaps a suitable place to draw attention to a tendency on the part of some workers to take rather dubious liberties with nomenclature when constructing their particular schemes of relationships. For example Heberer has in a number of works substituted the name *Australanthropus* for *Australopithecus* because he feels that a hominid ought not to have the suffix "*pithecus*" in its name. Weinert has used both *Giganthropus* and *Gigantanthropus* to replace the name *Gigantopithecus*. Heberer ('48) remarked that *Giganthropus* would be more suitable than *Gigantopithecus*, but used the latter term never-

theless. This was also done by Weidenreich but Ashley Montagu ('45) acted on Weidenreich's suggestion and uses the name *Gigantanthropus*. Weinert ('52, p. 325) has also remarked, in discussing the robust mandible (SK 12) from Swartkrans, that the name *crassidens* does not suit this specimen. He suggests "*crassicorporal*" as more suitable. These workers are apparently proceeding from the point of view that a name must tell something about the specimen to which it is applied. However desirable this may be, it certainly is not a generally applied rule. In some cases taxonomists have created a name which means nothing, being in effect simply a label consisting of a euphonious combination of letters of the alphabet. The prime function of a name is that of being a handy label enabling easy identification of a specimen under discussion. Manifestly, frequent alterations of a name to suit current ideas on the affinities of the specimen concerned is a wholly unnecessary complication in the already complicated subject of nomenclature. The affinities of a genus are indicated by the higher categories into which it is placed and it is therefore not necessary to try to do this by means of the generic name. Furthermore, according to the accepted rules of zoological nomenclature it is not legitimate to alter a generic or specific name unless it can be shown that the name has already been used generically or specifically in some other connection — whether this use was correct or incorrect, i.e. whether the name is now in good standing or is in the synonymy. To alter a name, as in the above cases, to suit the views of a particular author, is not allowed by the accepted laws governing the matter.

To return to *Meganthropus palaeojavanicus:* in most classifications which mention this form it is considered to be a hominid. But a certain amount of confusion arises here as to the exact meaning attributed to "hominid" in this instance. As far as one can determine most workers who have expressed a definite opinion that it is "hominid" mean euhominid. Weidenreich, for example, says ('45, p. 99): "I do not believe that *Meganthropus* is 'generically' different

from *Pithecanthropus,* as the name, when used in the strictly taxonomic sense, may suggest.'' Heberer ('51a, b) places only the australopithecines in the subfamily Praehomininae, and considers that all belong to a single genus ''*Australanthropus.*'' He therefore presumably considers *Meganthropus* to be a euhominid. Von Koenigswald is also of this opinion. For example he says (von Koenigswald, '50, p. 60) ''This giant form . . . must be placed within the line leading to modern man.'' Hennig ('50) and Ashley Montagu ('45) regard *Meganthropus* as a euhominid. Hennig apparently considers it to be more advanced and geologically younger than *Pithecanthropus* and *Sinanthropus* according to Chart IV which gives his ideas on primate relationships. Teilhard de Chardin ('51), without giving a detailed opinion, clearly also classifies *Meganthropus* in the *Pithecanthropus* group.

Table 2 gives some comparative dimensions of P_3, P_4 and M_1, including those of *Meganthropus.* In my opinion, as stated earlier, simple dimensions of teeth are characters having very low phyletic valency, to use an apt expression employed by Kälin ('46). They are used here simply to indicate into which size-group *Meganthropus* falls.

All dimensions are given in millimeters. M = module. The values for *M. palaeojavanicus, Plesianthropus, P. robustus* and *Pithecanthropus* B are in each case the dimensions of single teeth; in the other cases the dimensions are mean values.

From table 2 it is at once clear that there is an almost complete separation between the prehominids and euhominids. The only overlap is M_1 of *Plesianthropus,* the value for which falls in the euhominid range. It should be pointed out here that the *Plesianthropus* values are unsatisfactory. P_3 and M_1 belong in the same mandible while P_4 is an isolated tooth. Furthermore, P_3 is an incompletely developed germ and the dimensions given are certainly too low, though by only a small percentage. A single other molar is known which is probably M_1 and this has a module of 14.1 — which is more consistent with the other australopithecine values. Apart

TABLE 2

Comparative measurements of lower premolars and first molar

	P_1			P_3			M_1		
	Length	Breadth	M	Length	Breadth	M	Length	Breadth	M
M. palaeojavanicus (Weid.)	10.0	12.0	11.0	10.2	12.0	11.1	15.0	13.5	14.3
P. crassidens (Rob.)	9.7	11.7	10.7	11.0	13.3	12.2	15.0	14.3	14.7
Plesianthropus (Rob.)	9.4	10.2	9.8	10.0	11.3	10.7	13.2	11.2	12.2
P. robustus (Broom)	10.2	12.8	11.5	11.8	13.3	12.6	14.5	13.0	13.8
Sinanthropus (Weid.)	8.7	10.0	9.4	8.7	9.8	9.3	12.6	11.8	12.2
Pithecanthropus B (V. Koen.)	..	...	..	9.2	11.0	10.1	12.5	13.0	12.8
Australian (Campb.)	7.6	8.8	8.2	7.7	8.9	8.3	12.3	11.9	12.1
Modern White (Black)	6.9	7.9	7.4	7.1	8.0	7.6	11.2	10.3	10.7

from this one exception the dimension of the prehominid teeth are consistently larger than those of the euhominids. The dimensions of the *Meganthropus* teeth are all near the upper portion of the prehominid range and in no case do the modules approach those of any euhominids closely.

These figures bring out a point which ought to be mentioned; the size ratio $P_3 : P_4 : M_1$ is rather different in *Meganthropus* compared to that usual among the australopithecines. The size relation of these three teeth in *Meganthropus* is similar to that for the Australian aboriginal according to mean dimensions given by Campbell — the absolute sizes for the latter teeth are smaller, however. The australopithecines, on the other hand, have a relatively high value for P_4 compared to P_3. In figure 3 "curves" are shown illustrating these ratios in *P. crassidens* and the South African Bantu.

Three "curves" are given for *P. crassidens* where the measurements for the three teeth were taken on the same side of the same mandible. The three curves for individual mandibles represent the only mandibles available in which the relevant teeth are all present and undamaged. This figure shows that there is an appreciable amount of variation in the relative proportions of these teeth. The curve for SK 6 (the *P. crassidens* type mandible) differs considerably from the other two and agrees closely with that for *Meganthropus*. P_4 in SK 6 is not typical of this species in its structure but on the other hand it is of a type not infrequently found in modern man. Unfortunately it is not known how typical the *Meganthropus* II mandible is of the species as a whole. However that may be the relative proportions in this mandible are very similar to those in the *P. crassidens* type mandible. The 4 Bantu specimens were taken at random from a general collection and show a similar range of variation, in this character, to that found in *P. crassidens*.

How important this feature is — its phyletic valency — is a little difficult to assess. As demonstrated, there is a considerable degree of variation among the various hominids as well as among individual specimens of a particular form.

In the general reduction of a large dentition to a smaller one differential reductions in closely related lines are clearly not identical. As figure 3 shows, the relative size of these teeth, which is reflected by average figures, is composed of a variety of ratios. A single specimen is therefore an unreliable indicator of the average position. It is thus clear

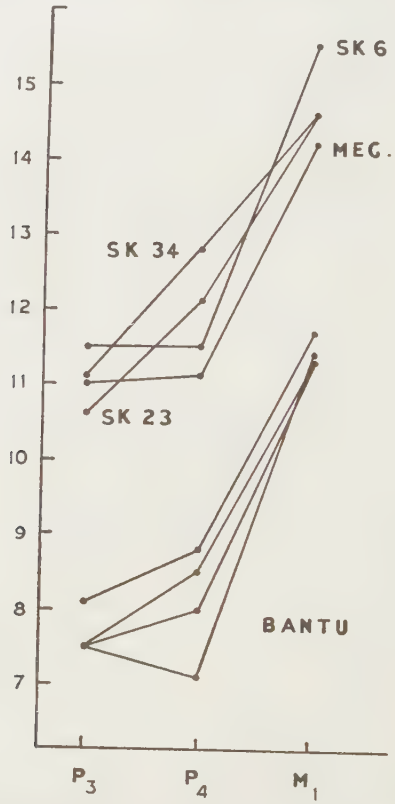

Fig. 3 Comparison of modules of P_3, P_4 and M_1 in *P. crassidens, Meganthropus* and Bantu.

that this character is not of great value — especially in this case where only a single *Meganthropus* mandible is known with the appropriate teeth in position.

More important than sizes and ratios is the morphology of the mandible and its teeth. The teeth will be considered first.

First premolar. In the australopithecines P_3 is a very interesting tooth which has a characteristic structure enabling ready identification. This structure has been discussed at some length, e.g. Robinson (in Broom and Robinson, '52; Robson, '52) and is best demonstrated by the excellent series of specimens of *P. crassidens.* The *Meganthropus* P_3 is a typically australopithecine tooth. The crown is asymmetrical when viewed occlusally. The anterior fovea is small compared to the posterior one and the distal wall of the latter is thickened. The distolingual region is enlarged so that the crown width is much greater distally than mesially. The lingual cusp is not situated at the point of maximal lingualward extension of the crown and is rotated mesiobuccalward. The buccal face has two well defined buccal grooves or depressions — the mesial one being more strongly developed. Much of the root is visible and it is of the form I have designated Type 3; there is a lingual or mesiolingual cleft but none distobuccally. In this case there is a well developed mesiolingual cleft below the lingual cusp and a depression down the mesial root just buccalward of the cleft. There is no sign of division on the buccal part of the root. All these features apply in detail to the majority of P_3 specimens of *P. crassidens.*

In figure 4 only one *P. crassidens* tooth is figured in occlusal view and minor differences are detectable between it and the *M. palaeojavanicus* tooth. In these minor features e.g. the slightly greater width across the tooth in the region of the anterior fovea, there is enough variation in the *P. crassidens* specimens to include the *Meganthropus* tooth. The only feature which cannot be so included is the fissure pattern in the posterior fovea, which differs in all cases from that in the *Meganthropus* specimen. This feature can, however, be exactly duplicated in *Paranthropus robustus.* In the mesial views small differences are also detectable, the chief one being the dipping down of the cervical line over the mesiolingual cleft. This region is not clearly defined in the cast in my possession, but it seems that no enamel peak is

present in the *Meganthropus* tooth — an observation supported by the drawings and photographs published by Weidenreich. This enamel peak appears to be constant in *P. crassidens,* but does not seem to occur in *Plesianthropus.*

The similarity of the two forms is clearly shown in figure 4. The *Meganthropus* tooth is therefore not only typi-

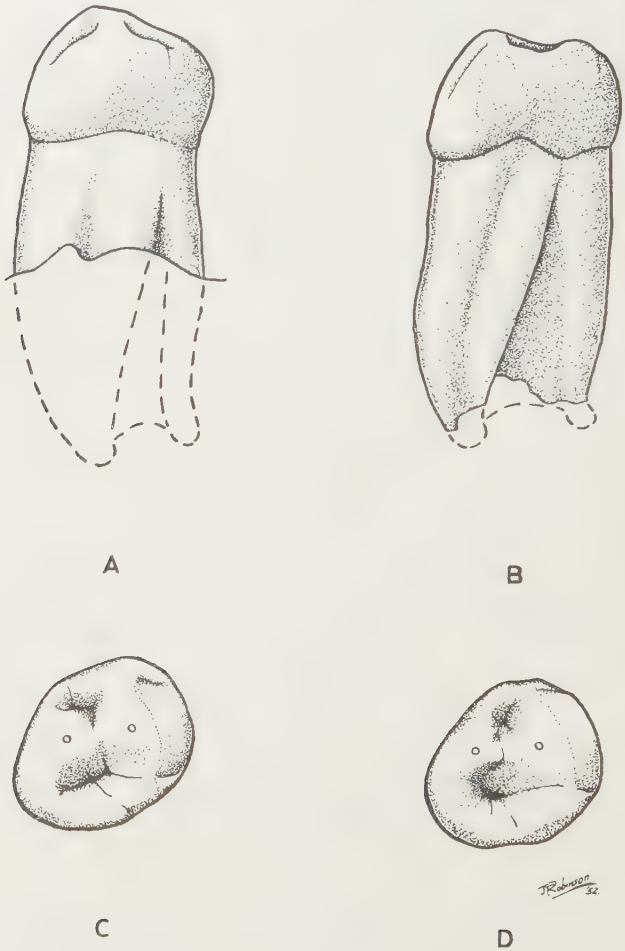

Fig. 4 P_3 in *Meganthropus* and *P. crassidens.* A. Mesial aspect, *Meganthropus.* B. Mesial aspect, *P. crassidens.* C. Occlusal aspect, *Meganthropus.* D. Occlusal aspect, *P. crassidens.* All × 2.

cally australopithecine in size and structure but in most features approaches the *P. crassidens* condition closely.

Unfortunately the homologous tooth is missing in the *Pithecanthropus* B mandible. The nearest to this is probably the *Sinanthropus* tooth. Tooth no. 82 is clearly constructed along very similar lines to the *P. crassidens* and *Meganthropus* teeth but in both size and root structure it is nearer the form found in modern man than are those of either of the other two. There are also distinct differences in the crown, especially in the structure of the lingual cusp which tends to be sharply differentiated. This is well shown in specimens 20 and 80.

Second premolar. In *Meganthropus* this tooth has a well developed talonid as well as two developed mesial cusps; one buccal and one lingual. The anterior fovea is appreciably smaller than the posterior one and the two are separated by the fused triangular ridges joining the two mesial cusps. When unworn the buccal mesial cusp was probably only slightly higher than the lingual one. The distolingual angle of the tooth is enlarged so that this region projects lingualward further than does the mesiolingual region. On the buccal face only slight indications of the two buccal grooves are apparent. The only part of the root which is visible is a portion of the buccal face. There is no trace of a division visible on the exposed portion.

In most fundamentals this tooth agrees in structure with those of the known australopithecines. In *P. crassidens* the anterior fovea is always smaller than the posterior one, the mesial cusps are subequal and sometimes are well separated but sometimes are joined at the base, separating the two foveae clearly. The talonid is always well developed and the distolingual angle is always more strongly developed than the mesiolingual one. There is, in *P. crassidens,* always a clearly defined distal buccal groove, but very slight traces of the mesial one. In *Plesianthropus* neither is strongly developed. In *P. robustus* and *A. prometheus* this feature resembles the condition in *P. crassidens.* These grooves are

always variable in whatever tooth they occur and even in modern man well defined distal buccal grooves, with no trace of mesial ones, occur on P_4. The *P. crassidens* form of this feature appears to be usual in *Sinanthropus* and appears to be present in P_4 of the *Pithecanthropus* B mandible. The two isolated specimens of P_4 of *P. crassidens* have separate mesial and distal roots. This does not appear to be the case in the *Meganthropus* tooth. However from the shape of the lingual face on the cast in my possession and judging from the photographs and drawings which have been published, it seems probable that there is a lingual division. This would mean that a condition similar to that of the P_3 root exists. This condition is to be expected in advanced prehominids or early euhominids and has been all but reached in at least one *P. crassidens* specimen (SK 23) and the only isolated *Plesianthropus* specimen (TM 1523). P_3 started from a completely double-rooted condition, which is still present in a recently acquired *P. crassidens* specimen, and in *P. crassidens* and *Meganthropus* has reached the Type 3 stage on its way to total reduction to single-rootedness. P_4, with a similar basic root structure, has probably done the same. As the *Meganthropus* P_4 is smaller than is usual among the known South African australopithecines it is reasonable to suppose that the root reduction process was also a little more advanced in this particular specimen. The homologous teeth in the *Pithecanthropus* B specimen and in *Sinanthropus* are, on the whole, similar to that of *Meganthropus,* but are a bit smaller, and lack the skewed shape of the crown due to hypertrophy of the distolingual angle, which is found in the latter specimen and all the South African australopithecines.

While there is thus not the identity between P_4 of *Meganthropus* and *P. crassidens* which there is between P_3 in these two forms, there is nevertheless a marked similarity. The similarity is greater between these two forms than between *Meganthropus* and either *Pithecanthropus* or *Sinanthropus.*

Weidenreich ('45) considered that there is a strong similarity between the *Pithecanthropus* and *Sinanthropus* teeth and that of *Meganthropus*. He mentions no. 89 of the *Sinanthropus* series as exhibiting "the same asymmetric form" as the *Meganthropus* P_4. However, tooth no. 89 is clearly highly abnormal, as shown by the other known specimens and in any case does not resemble the *Meganthropus* specimen closely. He also suggests that P_4 of the latter form is more symmetrical than that of *Pithecanthropus* B. This statement is clearly contradicted by the facts. The reverse is the case. The *asymmetry* of the *Meganthropus* tooth is its most interesting feature and clearly links it with those of the australopithecines, all of which exhibit the same asymmetry.

First molar. The dimensions given above show that this tooth is very robust and larger than the largest of any known euhominid.

Unfortunately the occlusal surface is considerably worn — dentine is exposed on the protoconid, hypoconid and hypoconulid — and little remains of the fissure pattern. However enough remains for adequate comparison of this tooth with others.

In shape the occlusal surface is longer than wide and is almost rectangular but with the distobuccal angle flatly rounded. This is in contrast to the *Pithecanthropus* B tooth in which the occlusal surface is more nearly square. The latter tooth is also a little unusual in having the width greater than the length. M_1 in *Sinanthropus* is more nearly like the *Meganthropus* tooth. As in modern man, however, the buccal grooves of the *Sinanthropus* tooth pass a relatively long way down the buccal surface and have no abrupt termination. The buccal contour of the occlusal surface is therefore not smooth. This is not the case in the *Meganthropus* M_1 where the buccal grooves terminate abruptly high up the buccal face. The mesial buccal groove terminates in a distinct pit; buccal to this the face bulges outward where a remnant of the buccal cingulum is present. From this pit

a groove runs forward horizontally and is joined by an almost vertical groove centrally placed on the side of the protoconoid. All of these features are typically australopithecine in character. In some cases in *Plesianthropus* the buccal grooves are sharply marked down to the pit and then continue as very faint grooves. Here also the vertical groove on the side of the protoconid is present in most cases. In *P. crassidens, P. robustus,* and *Australopithecus africanus* and *prometheus* the termination is abrupt and without noticeable continuation. In all cases, *Meganthropus* included, the mesial pit and associated bulge are more marked than those of the distal groove. *Sinanthropus* also has the remnant of protoconidal cingulum — or protostylid — but the mesial buccal groove does not terminate in a pit; it passes down the face, fading out gradually. The *Plesianthropus* condition is therefore intermediate between that of the other australopithecines and that of *Sinanthropus.* Of the occlusal surface it may be stated that there is nothing to differentiate between *Meganthropus* and the australopithecines in general. What remains of the fissure pattern can be matched in the australopithecine material, but this character is variable in details. There is a fairly clearly defined median lingual accessory cusp — a feature common among the australopithecines but, of course, not confined to them. Weidenreich ('45, p. 42) states "The contour of the margins indicates that there was a 'tubercle six' between entoconid and mesoconid."

Judging from what remains of the fissure pattern, from the position and sizes of the entoconid and mesoconid and the contour of the margin it seems most likely that a medium-sized tuberculum sextum was indeed present. Because of the degree of attrition this cannot be considered certain but on the evidence is highly probable. This is a feature of very great interest. In about a dozen specimens of M_1 of *P. crassidens* this cusp is present in every case. In one instance it is present only as a rudiment, in one or two cases as a large cusp and in other cases as a moderate-sized cusp.

The few specimens of *Plesianthropus* M_1 do not have any trace of this cusp, nor has the adolescent mandible of *A. prometheus*. On the other hand the Taungs *(A. africanus)* mandible has it and so, apparently, has the *P. robustus* mandible. It is therefore clear that the presence of a tuberculum

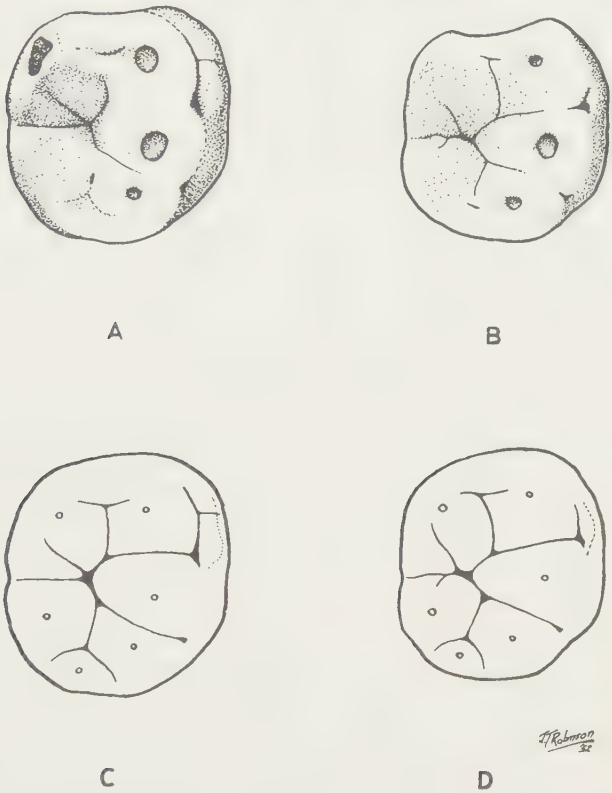

Fig. 5 Comparison of M_1 in A. *Meganthropus* and B. *P. robustus*. C and D are diagrams of the same teeth, unworn, to show the fissure pattern and cusp arrangements. All × 2.

sextum on M_1 is a character common among the australopithecines, and in the species in which M_1 is best known it is an invariable character as far as the material goes. In modern ethnic groups of man the tuberculum sextum is not very commonly found on M_1 — according to Hellman ('28) the Australian aborigines have the highest percentage occurrence:

8%. The probable presence of this cusp on the *Meganthropus* M_1 is therefore an important additional indicator of the australopithecine affinities of this specimen.

Weidenreich has also pointed out that the roots of this tooth are wide and relatively thin mesiodistally, that the mesial root is wider than the distal, and that *Sinanthropus* has similar roots. He also mentions that the mesial root is set vertically and is thinner, mesiodistally, than the distal root which slopes distalward and downward. Most of this is correct but examination shows that buccally the mesial root is thinner than the distal one while lingually the reverse is the case. This is true of the roots of some specimens of the *P. crassidens* M_1, but not of *Sinanthropus*. In all other features the roots of this tooth also resemble those of *P. crassidens*.

Here again the conclusion is clear: the similarity between *Meganthropus* and the australopithecines is much greater than that between the former and the known primitive euhominids.

The greater part of the canine alveolus is present in the *Meganthropus* specimen but the tooth itself is missing. Weidenreich deduced that the canine was relatively small. In a very brief account von Koenigswald ('50) mentions an isolated canine which, "is small and, . . . , in no way different from the canine of modern man, except for size." This presumably means that this tooth is similar to, but slightly larger than, that of modern man. Among the australopithecines the only forms in which the canines are known are *P. crassidens* and *Plesianthropus*. In the former the lower canine is the same as that of modern man in both size and structure. In *Plesianthropus* the canine is appreciably larger than that of modern man. One may therefore be fairly certain that this undescribed *Meganthropus* canine falls within the range exhibited in the known australopithecine material. *P. crassidens* has canines, both upper and lower, which resemble those of modern man considerably more closely than do those of *Sinanthropus*. In some cases the similarity with modern hominid canines amounts to absolute identity.

Corpus mandibulae. One of the most impressive features about the *Meganthropus* specimen is the massiveness of the corpus mandibulae. Weidenreich has, on the strength of this specimen and the three isolated *Gigantopithecus* teeth, spoken of these forms as giants and developed the thesis that modern man has descended from a gigantic type of early man.

He has reconstructed a mandible, without ascending ramus, and on this has taken measurements from which indices have been calculated. These and the dimensions are given (Weidenreich, '45) without qualification as genuine measurements. I do not propose to give a detailed analysis here of the

TABLE 3

Measurements of the corpus mandibulae

	WIDTH			HEIGHT		
	Symphysis	Ment. for.	M_2 M_3	Symphysis	Ment. for.	M_2 M_3
Meganthropus	25.5	28.0	26.3	47.0	48.0	45.0
P. crassidens						
SK 12	27.8	30.0	33.5	49.5	49.5	38.0
SK 23	24.5	22.0	25.0	42.5	41.0	34.7

characters of the *Meganthropus* specimen but will confine the discussion to points of similarity or difference between it and australopithecines. Only measurements made on the preserved portion will be used; some of the others are clearly wrong. In table 3 measurements are given (in millimeters) of the width and height of the body measured at three points (a) the symphysis; (b) the mental foramen; (c) the point of junction of M_2 and M_3.

The two *P. crassidens* specimens measured are the most complete and therefore most reliable for this purpose. In both mandibles the corpus is completely intact and undistorted on at least one side. A cast of the *Meganthropus* specimen was measured so that Weidenreich's figures were reproduced (his were obtained from a cast) and the Swartkrans

specimens were then measured in the same way so that the measurements are directly comparable. It must be borne in mind that no height measurements of the *Meganthropus* specimen can be accurate, nor is the third width value likely to be accurate. The only height value which will be nearly correct is the one taken at the level of the mental foramen, but even here the alveolar margin is missing. At the symphysis a good deal of the alveolar portion is missing and at the distal end of M_2 (a point which can only be estimated) only the ventral margin is present.

The *Meganthropus* values fall between those of the two *P. crassidens* specimens. The only exception is the height in the region of the junction of M_2 and M_3. Reference to the photographs of Weidenreich's reconstruction of the mandible shows the reason for this at once. The ventral corpus margin, below the position of M_2, trends upward quite markedly but Weidenreich has not continued this trend in the reconstructed portion. The ventral margin clearly should continue that upward trend for a greater distance before flattening out below the ascending ramus. The australopithecine mandibles and the Mauer jaw, all of which have a similar structure in this region, strongly suggest that Weidenreich's reconstructed height at this point is too great. The width of the body in this region is probably a few millimeters too small. Once more, the australopithecine and Mauer mandibles show that in this region a bulge is present fairly high up the outer face of the body where the leading edge of the ascending ramus meets the body. This has not been allowed for in Weidenreich's measurement, though the increase would only be slight. In the light of these considerations there is only one point at which the *Meganthropus* mandible is more robust than the SK 12 mandible: the ventral margin of the mandible is thicker than that of any *P. crassidens* specimens. The latter specimens are shaped like the Mauer mandible in this region while the *Meganthropus* specimen has a bluntly rounded margin.

Although the most robust Swartkrans mandible is a little more robust than that of *Meganthropus* there is little to choose between the two in size. The known *P. crassidens* mandibles vary appreciably in robustness: one mandible (SK 34) is as large as SK 12 in height but has only roughly half the thickness. The corpus height also varies from specimen to specimen. Attention may also be drawn to the fact that the available material strongly suggests that *P. crassidens* is not a giant form. The mandible is probably the most robust part of the creature. The innominate is larger than that usual in modern man but it can be matched in size by large male Bantu innominates. The finger bones and proximal portion of femur and one or two other fragmentary postcranial elements are not large but even a little small compared to those of normal specimens of modern man. The skull itself is neither particularly large nor thick-boned. Hence this form cannot be considered a giant, even though it is probably at least as large as, or perhaps larger than, any of the other known australopithecines. *Meganthropus* is therefore unlikely to have been a giant either.

Weidenreich ('45, p. 50) gives a series of diagrams of sagittal sections through the symphyses of a variety of fossil and modern pongids and hominids compared to that of *Meganthropus*. In this he demonstrates that, allowing for size difference, the section for the Mauer mandible is very similar to that of *Meganthropus*. He also gives a comparison with the section for *Paranthropus robustus* reproduced from a drawing by Broom ('38). The drawing by Broom is not suitable for this purpose because the symphysial region of the *P. robustus* mandible is so damaged that any drawing can be no more than a very general approximation to the true shape. Approximately a dozen mandibles have been recovered from Swartkrans and from these a good idea of the symphyseal region is obtained. A considerable degree of variation is manifested and I have chosen three to illustrate the main features. These were chosen with regard to excellence of preservation as well as degree of variation. In other

words the specimens chosen illustrate almost the whole range of variation but only good specimens have been used. The juvenile specimen (SK 61, with first permanent molar erupted) is particularly well suited as there has been no distortion or damage to the mandibular body. The other two specimens are fully adult. In the case of SK 6 only the lingual face of the symphysis is usable. In SK 23 the whole symphyseal region is present and only very slight distortion has resulted from the two halves of the jaw being pushed a little towards each other during fossilisation.

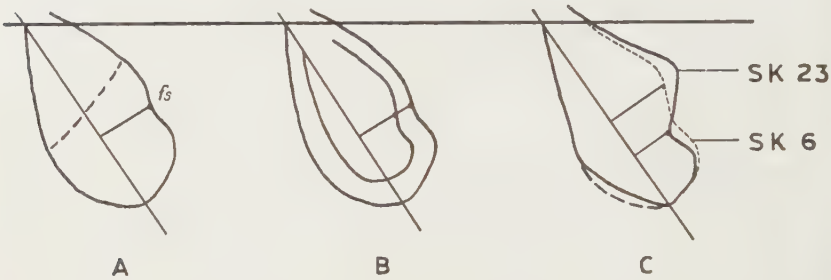

Fig. 6 Sagittal sections through the mandibular symphysis in *Meganthropus* and *P. crassidens*. A. *Meganthropus*, after Weidenreich. Portion above broken line not preserved. fs, foramen supraspinosum. B. Symphyseal section of SK 61 (juvenile) compared with that of *Meganthropus*. C. Symphyseal sections of SK 6 (type specimen) and SK 23. The lingual contour of SK 6 is very similar to that of *Meganthropus* except for the relatively high foramen supraspinosum. All two-thirds natural size.

From figure 6 it is manifest that the *Meganthropus* type falls within the range of variation of these specimens. In fact the SK 61 sagittal symphyseal section is an almost exact replica, on a smaller scale, of the *Meganthropus* one. This also includes the position of the foramen supraspinosum. The surface of the bone is undamaged and the foramen is plainly visible. Weidenreich has pointed out that the high position of this foramen is a hominid character. In SK 6 the position of the foramen is even higher while in SK 23 it is lower than in *Meganthropus*. The angle of inclination to the alveolar plane is the same as that of *Meganthropus*.

The position of the mental foramen in the latter specimen is very slightly further back than is customary in the known australopithecines. In the latter forms, when single, the mental foramen is situated below the interproximal space between P_3 and P_4; in the *Meganthropus* specimen it is below the distal half of P_4. In the australopithecines the position is variable.

In referring to *Meganthropus* von Koenigswald ('50) states, "That it is human is evident from the high position of the large foramen mentale . . . ," a point also made by Weidenreich ('45). If this is true then the same applies to *P. crassidens* which commonly has a single, large mental foramen situated at the same height as that of *Meganthropus,* roughly halfway between the alveolar and ventral margins of the corpus. In some cases the foramen is multiple — as is the case in the *Pithecanthropus* B mandible.

A mental spine appears to be present in the *Meganthropus* specimen. This structure is also present in *P. crassidens* and can be well seen in specimens SK 61, SK 6 and SK 25.

Markings for muscular attachment are very slight on the *Meganthropus* specimen but what appears to be a digastric fossa is present and, as Weidenreich puts it, "is partly niched in the notch." Weidenreich's writings on this point ('45) are rather obscure. He has defined a small depression ventral to the torus transversus as the "recessus digastricus" and considers it a unique feature. As is well known the digastric fossa is not always a depression but may be raised in parts. In this specimen the lateral part of the fossa appears to be raised and the "recessus digastricus" is the inner and anterior portion of it which is not raised. The fact that the broken edge of the mandible is not in the sagittal plane, ventrally, creates a mistaken impression that this "recessus" would meet that of the other side in the midline anteriorly. This is not so and the condition is really not unlike that in the Mauer mandible where, however, no part of the fossa digastrica is raised.

The digastrica fossa is plainly visible in some of the *P. crassidens* specimens, more especially SK 61, where it is typically hominid in position and appearance.

In analysing the character of the *Meganthropus* mandible Weidenreich lists the following characters which he regards as proving its hominid status:

1. The configuration of the symphyseal portion.
2. The development of a mental spine.
3. The high position of the foramen supraspinosum.
4. The position of the digastric fossa.
5. The high position of the mental foramen.
6. The homomorphic character of the canine group.
7. The form of the alveolar arch.

Of these points, 1 to 6 have been dealt with above and apply to *P. crassidens* and *Meganthropus* in equal measure. In connection with 7 it is considered that insufficient of the mandible is preserved and conclusions from extensive reconstructions are not here being considered. There is no detectable difference, in respect of this point, between the *Meganthropus* specimens and the equivalent parts of *P. crassidens* specimens.

For reasons generally similar to those here listed von Koenigswald ('50) also comes to the conclusion that *Meganthropus* is a hominid and " . . . must be placed within the line leading to man."

On all the available criteria it seems to me that the conclusion is unavoidable that, whatever *Meganthropus* is, there are no valid grounds for differentiating between it and the Australopithecinae. Point for point and feature for feature it has been shown here to resemble known australopithecines more closely than any other known hominids. Not only are all its characters australopithecine but it resembles *P. crassidens* in particular. Though the above criteria, which are used by Weidenreich and von Koenigswald to prove its hominid status, apply equally well to the australopithecines, neither of these authors will countenance the latter as in any way directly related to euhominids. In fact Weidenreich would

not even accept their hominid status, let alone any direct relationship to early euhominids.

In the final paragraph of his paper "Giant early man in Java and South China," Weidenreich concludes "The new finds do not offer a new clue as to the special anthropoid from which the hominids were derived. One of the characteristic primitive structures of *Meganthropus* recalls the condition of *Dryopithecus fontani* (Lérida), but the pattern neither of his teeth nor of the *Gigantopithecus* molars reveals any closer approach to the *Dryopithecus* and related types or to the Australopithecinae of South Africa." In another work ('46, p. 22) he says: I am of the opinion that they [the australopithecines] are not in the human line but are a special group which has preserved some of the original characters of the common stock from which man, as well as the other anthropoids, originated." In the same work (p. 56) he refers to the australopithecines as "that strange group . . . which shows the typical organization of anthropoids mixed with some human features." In the brief paper in the Robert Broom Commemorative Volume ('48) he makes it perfectly clear that the australopithecines are, in his opinion, pongids which have diverged from the line leading to man. What hominid characters they have, have "been retained from an original stock when they, like typical anthropoids, acquired special differentiations." He also points out that not enough material is known about them to be able to determine accurately their affinities. I find this whole attitude puzzling in view of the fact that from a cast of a single specimen of *Meganthropus* he was able to satisfy himself completely not only that this form was a giant, a hominid, congeneric with *Pithecanthropus* and ancestral to it but also that it was not related to the australopithecines. In view of the further fact that the characters of this specimen are typically australopithecine the logic of the whole position is rendered even more obscure. Even at the time he wrote the above there was much more information available about the australopithecines than about *Meganthropus*.

It has been demonstrated here that by Weidenreich's own criteria at least *P. crassidens* is a hominid with exactly the same status as *Meganthropus*.

DISCUSSION

The South African australopithecines are now remarkably well known for a fossil primate group. The number of specimens recovered is at least as great as that of all known fossil hominids from the East, including the tragically lost *Sinanthropus* material. Although most of the material relates to the skull, some very valuable and illuminating postcranial material is known. Careful evaluation of the material has shown beyond question that a well defined group is here being dealt with; they may be distinguished with the greatest of ease and certainty from all known fossil and modern pongids and also, but less sharply, from all known euhominids. However there is clearly much greater affinity between the australopithecines and euhominids than between the australopithecines and any other primate group at present known.

Knowledge regarding the fauna associated with them and the geology of the deposits is also increasing considerably. From available faunal, geological and archaeological evidence the geological age of the known forms may be fixed with reasonable certainty; the age must be no earlier than upper Pliocene and no later than lower Pleistocene. In all probability the known forms ranged from somewhere in the upper Pliocene through into the Villafranchian, as the deposits so far excavated appear to cover a relatively long period judged by Quaternary standards. However, the differences between forms such as *P. crassidens* and *Plesianthropus* are of a nature which suggests that they represent two lines which were evolving separately and had been for a considerable period. Clearly also the whole group was abundant in South Africa at the time mentioned above. *Telanthropus* is manifestly very closely related to the australopithecines but seems to have already reached the euhominid grade of organization. These facts argue in favor of the australopithecine

group having been in existence for a long time prior to the existence of the known forms. It would therefore be surprising if they were confined to South Africa.

The discovery, at almost the same time, of the so-called *Meganthropus* from East Africa and of *Meganthropus* from Java is of very great interest and significance. The characters of these two forms are similar to those of the South African australopithecines beyond peradventure. In every character — with a few exceptions of no special significance — they fall within the range of variation of known australopithecines. The degree of similarity is remarkable in view of the fact that one was found some 3,500 odd miles to the north of the australopithecine area of South Africa and the other three times that distance across the Indian Ocean to the east. The conclusion is therefore fairly obvious that we are actually dealing with scattered members of a well defined group which was almost certainly spread, at some time in the past, over the greater part of Africa and Asia and probably Europe also. The ages, as far as they can be determined, are very similar, the Javanese specimen probably being a little later than the others. Some isolated teeth obtained from Chinese drugstores by von Koenigswald show many similarities to the other members of this group and may be additional evidence for their wide distribution in the past. As many of these teeth have not been described systematically and little is known about them in general, little weight is attached to them for the time being. Broom was of the opinion that *Gigantopithecus blacki* is an australopithecine too. In view of the scantiness of the remains it would be unwise to draw any very definite conclusions though it does seem possible that it is a rather aberrant member of this group.

As already mentioned Weidenreich considers *Meganthropus* to be ancestral to *Pithecanthropus* and thus to modern man. From his published opinions it would be correct to say that he believed *Meganthropus* to be a direct ancestor of the modern Australian aboriginal. It has also been mentioned that von Koenigswald is of the opinion that *Meganthropus*

cannot be considered to belong to "a mere sidebranch of mankind, but must be placed within the line leading to modern man." However he believes that the australopithecines are hominids but not ancestral to *Pithecanthropus* and hence — presumably — to modern man (von Koenigswald, '51). He also considers that the australopithecines are *certainly* no older than *Pithecanthropus,* a viewpoint which is probably mistaken regarding the known forms but which is in any case almost certainly more true of *Meganthropus* than of the South African australopithecines. If the South African forms are to be dismissed on this ground from ancestry to modern man, so must *Meganthropus.* On the other hand, as the morphological characters of *Meganthropus* are the same as the corresponding ones of the South African forms and as both Weidenreich and von Koenigswald consider *Meganthropus* to be ancestral to modern man, then on these grounds so must be the South African forms.

There is a curious feature about the arguments concerning the possibility of certain forms being ancestral to others. It is commonly stated, for example, that the australopithecines cannot be ancestral to man because the known forms lived too recently. To me this a strange sort of argument. It is obvious — it is almost naive to mention it — that the australopithecine group did not come into existence at the time the oldest (geologically speaking) known specimen in our collections lived. Nor did the group cease to exist at the time of death of the geologically youngest specimen present in our collections. It has already been suggested above that good reasons exist for considering that the australopithecines had been in existence for a very long time prior to the life of the oldest of our specimens. It is also equally obvious that a group does not necessarily, or even usually, become extinct at the point where it gives rise to a new line of evolution. For example reptiles gave rise to mammals and reptiles are still in existence now. A better example is the fact that early Tertiary prosimians gave rise to the higher primates and yet some living prosimians are very lit-

tle altered from known early Tertiary forms. If an australopithecine gave rise to the early euhominids there is no conceivable reason why early euhominids and australopithecines should not have been coeval. The particular euhominid ancestor would naturally not be in existence at the same time as its descendant. If it is a fact that the characters of the australopithecines, in general, are such that the early euhominid characters are logically and easily derived from them but the time interval between the known members of the two groups is either too short or non-existent, it simply means that the known forms of prehominids are not the actual direct ancestors themselves but their very close relatives.

In the history of the vertebrates as we now know it, it seems to have been a common occurrence that the ancestors of a descendant group arose early in the history of the parent group. The reptile-mammal bridge is a good example. The mammal-like reptiles which gave rise to the early mammals arose and flourished early in the history of the reptiles. The great adaptive radiation giving rise to all the manifold forms of terrestrial, marine and aerial reptiles reached its maximum very much later. It appears that that section of the group which is to proceed to the higher grade of organization often does so at a relatively rapid rate compared to the slower forms which diversify but do not change their essential nature. This would presumably also be true of the euhominid ancestor or ancestors. It or they would rapidly pass from the early australopithecine stage to the euhominid (as *Telanthropus* probably did) leaving the other, slower australopithecines to spread and adapt themselves without ever rising beyond the australopithecine level.

To find prehominids and euhominids living together at any particular time in the past is therefore no more than should be expected. While the South and East African, Javanese and possibly Chinese australopithecines are thus representatives of a group which are the most suitable precursors of the euhominids it is likely that earlier deposits than the known ones will have to be sought to find the early eu-

hominids in the process of changing from the prehominid to the euhominid stage. Even then identification of the actual prehominid ancestor of the euhominids will be very difficult. Some workers seem to consider that an ancestral euhominid must have euhominid characters, which is naturally an impossible contradiction. However choosing a particular known australopithecine such as *Meganthropus* as a direct ancestor is almost certainly incorrect. It is perhaps never possible to do more than point to a particular species as a representative of the ancestral group. When the australopithecines are better known as the result of further discoveries it may be possible to point to a particular form, more euhominid-like than the other known forms, as a member of that subsection of the australopithecines from which euhominids did arise.

CONCLUSIONS

1. The characters of the so-called "*Meganthropus*" *africanus* are almost identical with those of known South African australopithecines, especially *Plesianthropus*.

2. In view of this fact and the further fact that no upper premolars are known of *Meganthropus palaeojavanicus* there is no valid reason for referring the East African form to the genus *Meganthropus*.

3. Every single important character of the *Meganthropus* II mandible is typically australopithecine in nature, resembling *P. crassidens* in particular.

4. The South and East African forms as well as *M. palaeojavanicus* are therefore representatives of a once widely spread australopithecine group.

5. This group is ancestral to the euhominid group, though naturally *all* the members of the former are not ancestral to the latter and it is unlikely that *the* ancestor has been found.

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PRIOR AND SIMULTANEOUS PUBLICATION.— The Editor is chagrined to find that, doubtless because of the author's failure to notice the Journal's stated rule against the practice, the article by Rodahl in the December issue, "The body surface area of Eskimos as determined by the linear and the height-weight formulas" had also appeared in the November, 1952, issue of the Journal of Applied Physiology, and in fact had a prior if limited circulation as of May, 1952, as a publication of the USAF School of Aviation Medicine. It develops that the author inquired of both editors simultaneously in March, 1952, as to how to prepare his material for publication in their respective journals, and sent in the same article, except for editorial style, to each, again simultaneously. Both editors required certain changes, of a somewhat similar nature and, after provision in our own case for deposit of supplementary material with the ADI, the manuscript for this Journal was sent to the publisher September 25. Neither editor was aware of the duplication before publication, and in fact the Editor has heretofore had no screen, except for chance, by which such cases may be avoided. Therefore it is hoped that all readers and prospective authors will, in this time of limited and costly space, take careful note of the rule against simultaneous publication in the "Notice to contributors."

BLOOD GROUP FACTORS IN ANTHROPOID APES AND MONKEYS

II. FURTHER STUDIES ON THE Rh-Hr FACTORS

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In a previous paper (Wiener, '52) evidence was presented for the presence of factors Rh_0 and hr′ in the blood cells of a chimpanzee, "Pan" (cf. Wiener and Wade, '45). Moreover, it was shown that the factors Rh_0 and hr′ in this chimpanzee's blood are not identical with the corresponding factors of human blood. Thus, anti-Rh_0 and anti-hr′ agglutinating sera of high titer for human red cells failed to clump the chimpanzee's red cells in saline media; but, when the chimpanzee's cells were treated with proteolytic enzymes they were strongly agglutinated, the titer of the antisera being almost the same for chimpanzee and human red cells. The purpose of the present study is to extend these observations to additional chimpanzees as well as to lower primates. Accordingly, this paper will describe briefly the results of tests to date on blood from 4 chimpanzees, two spider monkeys, and a rhesus monkey as compared with those of human blood.

MATERIALS AND METHODS

Blood was collected aseptically by venipuncture, part of it placed in a dry sterile test tube and part mixed with a preservative solution containing sodium citrate and glucose. The blood was shipped by air mail to New York City where the actual tests were carried out. Blood suspensions were prepared, washed once with saline solution, and diluted with

saline solution to form a 2% concentration in terms of red cells. The enzyme-treated blood suspensions were prepared as follows: The red cells were washed three times with saline solution, and then 9 volumes of packed washed cells were mixed with one volume of a 1% saline solution of ficin and the mixture incubated at body temperature for one hour. The action of the enzyme was stopped by washing the cells with saline solution, and a 2% suspension of the enzyme-treated cells was used for the tests.

All the tests were carried out quantitatively by testing the cell suspensions (untreated or enzyme-treated) of each subject with progressively doubled dilutions of the antisera. The results are expressed in terms of units of titer, namely, the reciprocal of the highest dilution giving a distinct or so-called one plus reaction, that is, clumps containing 10 or more cells upon microscopic examination.

Since the specimens of blood from different chimpanzees and monkeys arrived at different times, the actual experiments were carried out in installments. The tables which will be presented, therefore, represent a composite of a number of such experiments. As a result there are irregularities in the results which may be attributed to the variations in the sensitivity of the tests as carried out on different days. Fuller details concerning technique can be found in earlier papers (Wiener, '43; Wiener, Nappi and Gordon, '51).

RESULTS

Rh-Hr factors. In table 1 are summarized the results of tests with a number of anti-Rh_0 sera from sensitized human subjects. It will be seen that the blood from all 4 chimpanzees gave similar reactions. As previously reported, in saline media chimpanzees' cells gave at most only weak clumping even with antisera having a high titer for Rh-positive human cells in similar tests. On the other hand, when the cells were enzyme-treated, the titer of the antisera for chimpanzees' cells was almost the same as for human Rh-positive cells, or only slightly lower. These results indicate that the blood of

all 4 chimpanzees contain a factor very similar to but not identical with the human blood factor Rh_0. On the other hand, blood cells from a rhesus monkey, even when enzyme treated, gave at the most only weak reactions with the Rh_0

TABLE 1

Reactions of ape and monkey blood cells with anti-Rh_0 sera[1]

BLOOD OF	SERUM NO. 1		SERUM NO. 2		SERUM NO. 3		SERUM NO. 4	
	Sal.[2]	E.T.C.[3]	Sal.	E.T.C.	Sal.	E.T.C.	Sal.	E.T.C.
Human								
Rh positive	0	1700	10	130	65	100	0	55
Rh negative	0	0	0	0	0	0	0	0
Chimpanzees *(Pan satyrus)*								
Pan (group O)	0	1800	0	95	1	32	0	20
Ken (group A)	0	2500					0	40
Alan (group A)			3	32	2	22		
Art (group A)	0	680					0	45
Rhesus monkey *(Macaca mulatta)*	0	12			2	2	0	4
Spider monkeys[4] *(Ateles geoffroyi)*								
Male	0	8					4	16
Female	0	4					9	24

[1] Composite of several experiments. All tests carried out at body temperature.

[2] Sal. = tests on 2% suspensions of unmodified cells in saline media.

[3] E.T.C. = tests on 2% suspensions of cells treated with ficin.

All tests were carried out quantitatively, by titrating the antisera against the red cells of the subject. The figures represent the reciprocal of the highest dilution of serum producing distinct clumping of the cells.

[4] The reactions with blood of this species may be due to heteroantibodies other than anti-Rh_0 present in the human antisera.

antisera, indicating that the Rh_0 factor in this monkey is quite different from the Rh_0 factor in human blood. Blood from two spider monkeys was also tested and gave moderate reactions with the Rh_0 antisera, which could however be attributed to the natural heteroagglutinins present in human sera. These results, therefore, demonstrate clearly the evolution of the

Rh_0 factor, the biochemical similarity being greatest in chimpanzees, as is to be expected.

The results of the tests with anti-hr′ sera were similar, as shown in table 2. Thus, the blood of all 4 chimpanzees behaved alike; the reactions demonstrated the presence of a blood factor similar to but not identical with the human factor hr′. The blood from the rhesus monkey failed to clump

TABLE 2

Reactions of ape and monkey blood cells with anti-hr′ sera[1]

BLOOD OF	SERUM NO. 1		SERUM NO. 2		SERUM NO. 3	
	Sal.[2]	E.T.C.	Sal.	E.T.C.	Sal.	E.T.C.
Human						
hr′ positive	0	300	0	48	32	170
hr′ negative	0	0	0	0	0	0
Chimpanzees						
Pan	1	350	0	96	½	140
Ken			0	48	0	130
Alan			0	190	2	120
Art	0	112	1	60	0	44
Rhesus monkey	0	0	0	0	0	0
Spider monkeys						
Male			1	5	2	2
Female			1	4	2	3

[1] See footnotes to table 1.

[2] The anti-hr′ serum used by Wiener and Wade ('45) was exceptional, since it clumped chimpanzee cells in saline media.

in hr′ antisera even when enzyme treated. The blood from the spider monkeys gave weak reactions with the anti-hr′ sera, but this could have been due to the species specific heteroagglutinins present in normal human sera. Thus, if the blood cells of the rhesus and spider monkeys contain a factor corresponding to the hr′ factor at all, this must be considerably different from the human hr′ factor. The corresponding factor in chimpanzees, on the other hand, as to be expected, is quite similar to the human hr′ factor.

The A-B-O groups. The opportunity was taken to test the blood of the chimpanzees and monkeys for the A-B-O blood factors. The results confirmed earlier observations that chimpanzees have blood groups indistinguishable from the human A-B-O groups. Three of the chimpanzees proved to belong to group A, and one to group O.

The serum of the rhesus monkey contained an anti-A agglutinin and no anti-B agglutinin, but no B agglutinogen was demonstrable in the red cells. In previous studies (Candela, Wiener and Goss, '40; Wiener, '43) the presence of B-like substances was demonstrated in the saliva and organ extracts of rhesus monkeys, and this accounts for the absence of natural beta agglutinins from the serum.

Also in the case of the two spider monkeys the sera contained anti-A agglutinins but no anti-B. In tests on the spider monkeys' red cells, anti-A sera of human origin as well as anti-A sera prepared by immunizing rabbits gave negative results. On the other hand, strong clumping was obtained with anti-B sera of human origin, but negative reactions with anti-B sera prepared in rabbits. Thus, the red cells of these two spider monkeys contain a B-like blood factor, which accounts for the absence of anti-B agglutinins from the serum (cf. Wiener, Candela and Goss, '42). Landsteiner and Miller ('25) had previously demonstrated the presence of B-like blood factors in blood cells from New World monkeys, while no B-like factor could be demonstrated in red cells of Old World monkeys.

M-N factors. Since the evolution of the M-N factors had been worked out in detail in earlier investigations (Wiener, '38; Landsteiner and Wiener, '37; Wiener, '43) detailed tests for these blood factors have not been carried out in the present study. As pointed out in the previous paper, the only significant new finding is that the M-like agglutinogen in chimpanzee blood, like the corresponding agglutinogen in human blood, is inactivated by proteolytic enzymes.

SUMMARY AND CONCLUSIONS

The blood cells of 4 chimpanzees were tested for the Rh-Hr blood factors with antisera of human origin. All 4 possessed factors Rh_0 and hr′, but the Rh-Hr blood factors in chimpanzee cells were demonstrable only after treatment of the cells with proteolytic enzymes. This indicates that these Rh-Hr factors in chimpanzee blood are similar to but not identical with the corresponding factors of human blood. On the other hand, Rh-Hr factors could not be demonstrated convincingly in red cells from a rhesus monkey or two spider monkeys even after enzyme treatment. This may seem surprising, considering that the first anti-Rh sera were prepared by immunizing rabbits and guinea-pigs with rhesus red cells. (In fact, that is how the Rh factor derived its name.) The findings are readily understandable when one considers that the Rh agglutinogen of rhesus blood is probably quite different chemically from the corresponding substance in human blood. Accordingly, these studies on the Rh-Hr factors in apes and monkeys provide further evidence of biochemical evolution.

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ADDENDUM

While this paper was in press 4 additional chimpanzees were tested, namely, Alf (group A), Banka (group A), Web (group A), and Flora (group A). The red blood cells of all these 4 additional chimpanzees reacted with anti-Rh_0 and anti-hr′ sera in the same way as the 4 described here. Moreover, tests with sera containing rh′ and rh″ antibodies without anti-Rh_0 gave negative or doubtful reactions, indicating that either rh′ and rh″ factors are not present in the blood of these chimpanzees or, if present, are quite different from the corresponding factors in human blood. Tests for factors Rh_0 and hr′ by the anti-globulin technique have confirmed the results obtained using enzyme-treated cells (Wiener and Gordon, '53). Moreover, tests with autoantibodies from patients with acquired hemolytic anemia (Wiener, Gordon and Gallop, '53) further confirm the close biochemical relationship between bloods from chimpanzees and man.

WIENER, A. S., AND E. B. GORDON 1953 Quantitative test for antibody globulin coating human blood cells and its practical applications. Am. J. Clin. Path. (in press).

WIENER, A. S., E. B. GORDON AND C. GALLOP 1953 Studies on autoantibodies in human sera. J. Immunol. (in press).

Nutritionally Oriented Anthropometry.— [The use of somatotype ratings for estimation of body fat] appears to be a devious and inefficient route, except under special conditions in which direct measurements on the living man were not or could not be made. For these conditions a system of ratings and measurements (based on photographs) is needed that is more directly focused on the evaluation of individual differences in the basic anatomical components of the body than are Sheldon's "components" of the body type. It is the estimation of the absolute and relative amount of fat — which accounts for the largest part of the differences among adult individuals — of muscles, and of bones, which is the principal concern of nutritionally oriented anthropometry.

Elsewhere [Brit. J. Nutrition, vol. 5, p. 194, 1951] equations were developed for predicting total fatness on the basis of measurements of skinfolds, varying in thickness as a result of different amounts of subcutaneous adipose tissues. This is a simple, objective, and rapid procedure. For younger men the coefficient of multiple correlation between specific gravity and skinfolds was 0.871, for older men 0.743, using skinfolds measured at three and 4 points of the body surface, respectively. The standard errors of estimate of the specific gravity are 0.0072 and 0.0086.— Josef Brožek and Ancel Keys. Body build and body composition. Science, vol. 116, no. 3006, pp. 140–142, August 8, 1952.

Duffy Factor in Blood Transfusions.— The Duffy factor is present in the red cells of 65% of the white population, the remaining 35% being Duffy negative reactors. Random sampling of the Negro population in New York City by Miller, Rosenfield and Vogel and also by us revealed a pronounced difference in the incidence of the Duffy factor in this group, only about 20% being Duffy positive reactors. That the Duffy factor is antigenic is demonstrated by the observation that when persons with a negative Duffy reaction are given transfusions of Duffy positive red cells specific antibodies (anti-Fy^a) may develop in significant titer. The Duffy factor, however, is probably a relatively poor antigen, for, though hundreds of thousands of Duffy negative reactors are given Duffy positive blood each year, only a small number of cases of specific immunization have thus far been detected.— J. B. Hutcheson, J. M. Haber and A. Kellner. A hazard of repeated blood transfusions. Hemolytic reaction due to antibodies to the Duffy (Fy^a) factor. J. Am. Med. Assn., vol. 149, no. 3, May 17, 1952, pp. 274–275.

A COLLABORATIVE GENETICAL SURVEY IN AINU: HIDAKA, ISLAND OF HOKKAIDO

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TWO FIGURES

In a recent paper Simmons, Graydon, Semple et al. ('51) presented the results of serological investigations on 678 Marshallese. This paper provided references to earlier blood grouping data published by these authors for the Pacific, and to methods employed in testing for each genetical character.

The present paper which was made possible by Australian, American and Japanese collaboration deals with 8 genetical characters in Ainu and Ainu-Japanese as follows:

1. A_1-A_2-B-O blood groups.
2. M-N-S blood types.
3. Rh blood types.
4. Lewis blood group and correlation with A-B or H substances in saliva.
5. P blood group.
6. Duffy blood group.
7. Kell blood group.
8. Ability to taste phenyl thiocarbamide.

A number of earlier investigations on the A-B-O blood groups, and one investigation on the M-N types in Ainu have been tabulated by Boyd ('39). An examination of the A-B-O frequencies shows variation in q the gene for group B and

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this will be referred to later in the text. In Ainu tested at Shizunai the M-N frequencies were $m = .423$ and $n = .564$.

There are many reports on the A-B-O and M-N frequencies in Japanese. Amongst the more recent investigations, Graydon, Simmons, Heydon and Bearup ('45) reported testing 400 pure Japanese mostly from Honshu for A-B-O groups, subgroups, M-N types, and the Rh factor. Of the 400 samples tested 399 (99.75%) were Rh positive with a serum subsequently proved to be anti-Rh_0 (anti-D). No Rh typing sera were available when these tests were made. Waller and Levine ('44) and Miller and Taguchi ('45) tested 150 and 180 Japanese respectively, resident in the U. S. A., for their Rh types. While each reported the absence of type Rh_0 and the presence of 1% or less Rh negative the former found 37.4% of type Rh_1 and the latter 51.7%. Chown, Okamura and Peterson ('46) also Rh typed 217 unrelated Canadian Japanese in a group of 606 tested. The calculated Rh gene frequencies will be referred to later in the text.

The following notes on the Ainu were written by one of us (S.K.) who has made a close study of this population.

THE AINU

The Ainu are an interesting and unique racial group which until recent years has continued to lead a stone age existence in Hokkaido, Japan. Anthropologically and ethnologically the Ainu are as remote from other races as their native island is isolated from the rest of the world. They are one of the least understood races of mankind. Where this race originated, how it came to exist in its present habitat and its relationships with other peoples are outstanding racial problems.

The total Ainu population, according to statistics of the Japanese government, is approximately 15,000, of which however a large majority are mixed with Japanese by intermarriage. Less than 3% seem to be pure Ainu exhibiting the typical characteristics of this race. Their numbers are now dwindling rapidly and they will soon be extinct.

The most conspicuous constitutional characteristic of the Ainu is their hairiness and they are thought to be the most hairy race in the world (see fig. 1). However, this applies only to the pure Ainu, as those who are mixed with the Japanese have lost their hairiness. The hair of the head is black, coarse and wavy. The stature is small, under 5′ 2″ on the average, and slightly less even than that of the Japanese. The skin is brown and the mixture of yellow colors which is a feature of Mongoloid races is very slight, or absent. The Mongolian spot is very rarely seen on the back of the pure Ainu infant. The Ainu have unusually broad, short faces with long moustaches and beards, beetling eyebrows and large, deep sunken, light brown eyes. The eyelashes are thick and long and the Mongolian or epicanthic fold is rarely seen in the pure Ainu. The nose, mouth and ears are large, and the lips are quite thick. The head is large, long and low; the average circumference of the neurocranium, determined by Kodama ('40) on 17 male Hidaka crania, is 542.2 mm, and that of the diameter, antero-posterior maximum, is 190.9 mm, figures which are among the highest in the world. The cephalic index of these Ainu skulls averages 75.8 showing a marked tendency towards a dolicocephalic form. The neck of the Ainu is short and the chest is wide and thick. The arms are longer than those of the Japanese both absolutely, and also in relation to stature; the legs are relatively short in comparison with the trunk.

The constitutional characteristics and general appearance of the Ainu suggest a Caucasoid type and indeed the most widely accepted hypothesis is that they were originally proto-Caucasians who migrated to Hokkaido at some remote time. Two possible routes of their migration have been suggested: (1) through Siberia direct to Hokkaido, (2) along the southern coasts of Asia to the Malay peninsula, Okinawa and finally to Hokkaido.

It has been generally thought that the Ainu were aborigines of Honshu, the main island of Japan, and that they occupied all Japan proper before being driven northwards by the Japa-

Fig. 1 Male Ainu, 57 years old. Chieftain, Kitami district, Hokkaido. Photograph taken 1912 by S. Kodama.

nese. However, recent anthropological excavations have shown that stone age skulls found in Honshu are entirely different from those of the Ainu; for example, the former are brachycephalic and the latter dolicocephalic. After considering the available evidence the writer (S.K.) has reached the conclusion that the Ainu lived from the beginning chiefly in Hokkaido and Sakhalin, and therefore are not to be regarded as aborigines of Japan proper.

In view of this opinion, it is perhaps fitting that the views of certain authorities given by the Encyclopaedia Britannica ('47) should also be quoted.

Volume 1, page 499: "Ainu, who are racially closely akin to, if not identical with, the Neolithic inhabitants of Japan are now very reduced in numbers and live in Hokkaido, the northern island of Japan, in part of Saghalien, and have kinsfolk in the Ryukyu archipelago.". . . (It is reported that there are also Ainu in the Kurile Islands.)

"Physically they are probably the remains of an old Proto-Nordic population which was once widely spread over Northern Asia, and are certainly the relics of a very old human stock.". . .

"The Ainu religion is closely akin to the animistic religion practised by various primitive peoples of Northern Asia, and they are particularly liable to that peculiar kind of religious ecstasy known as Arctic hysteria. One of their special cults is that of the bear."

Volume 2, page 530: "The oldest known inhabitants [of Japan] are the Ainu". . ."their wars with the Japanese are historical". . ."Authentic history hardly begins until the 6th century A.D."

Volume 12, page 901–902: "These people — the Ainu — are usually spoken of as the aborigines of Japan. They once occupied the whole country but were gradually driven northwards by the Manchu-Koreans and the Malays or Indonesians until only a handful survived in the northern island of Yezo (Hokkaido)". . ."The Ainu though the small surviving element now lives apart have left distinct traces upon their con-

querors''. . .''the evidence of place names shows that they once occupied the whole country including Kyushu.'' . . .

Reference is also made to long wars between the Ainu and the Japanese ''. . . the centuries long struggle with the Ainu.''

Sternberg ('29) after considering the physical, social and cultural characteristics of the Ainu in relation to their northern neighbors and races of the south seas, claimed that there was nothing to connect the Ainu with the polar people, the Siberian tribes or with China or Korea. He believed that the physical type of the Ainu could be classed as a variety of the Australoid long-headed, bearded race, representatives of which were to be found in Australia, South India and Western Oceania. Peculiar traits of their civilization and language were to be found in Indonesia, the Philippines and Formosa.

MATERIALS AND METHODS

The methods employed in the field for the collection of samples and the technical methods of testing in the laboratory at Melbourne, Australia, have been described by Simmons, Graydon, Semple and Taylor ('51), Simmons ('49), Simmons and Graydon ('50), Simmons, Semple and Graydon ('51).

Blood and saliva samples were collected in the province of Hidaka, Hokkaido. The initial field expedition from November 7–19, 1950, collected three series of samples — series I, 1–100; series II, 101–250; and series III, 251–437. With few exceptions the blood samples arrived in Melbourne free from haemolysis, but those of series II were lost due to the containers being placed in a freezer. The frozen samples haemolyzed when they were thawed out. Steps were taken immediately to attempt replacement of all samples of series II as many of these had corresponding saliva samples. Unfortunately, a second field expedition was not possible at the time, and it was not until November, 1951, that series II was replaced. Many of the original individuals were again located, but several individuals not previously included were taken

into the series. In this repeat series a total of 155 samples was collected, and although 6 to 13 days old when received for testing, not one of the 155 samples showed haemolysis.

At the time of collection of samples each individual was listed in the genealogical data recorded as Ainu or Ainu-Japanese. The individuals listed as Ainu were those regarded by one of us (S.K.) as being "pure" Ainu, while those recorded as Ainu-Japanese were Ainu subjects in whom evidence of Japanese admixture, however slight, could be detected or was admitted by the individual on questioning. The Ainu themselves claim to know whether they possess Japanese blood, as Japanese migration into this area has taken place largely within the last 100 years. It was observed sometimes that an individual who would be regarded anthropologically as "pure" Ainu was found in a so-called mixed Ainu family.

The province of Hidaka is in the extreme southeastern corner of Hokkaido and covers a comparatively narrow coastal strip running northwest to the Iburi border (see fig. 2). The collection of samples commenced at Samani, a coastal town in the southeast, and ended at Osachinai, a town about 18 miles inland near the Iburi border. The distance of the coast line covered from Samani to near the border was approximately 64.5 miles. The names of the towns, villages or hamlets visited are shown in table 1.

The areas covered for each series of samples can be pinpointed as follows:

Series I: From Samani and Okada to Ikantai, and inland to Anecha and Nobuka.

Series II: The adjacent coastal area extending from Ikantai to Shizunai and inland to Noya.

Series III: From Shizunai to near the Iburi border and thence inland along the Sarugawa approximately 18 miles to Osachinai. Series I covered about one-fifth of the coastal distance traversed, while Series II and III would each represent about two-fifths.

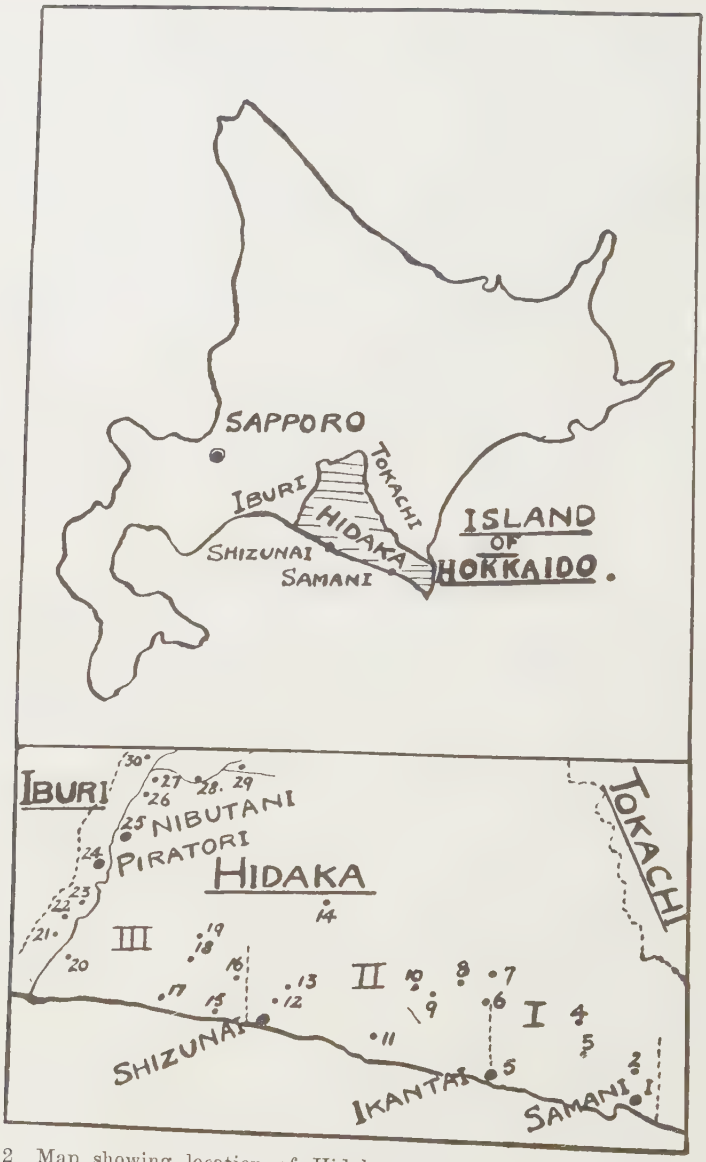

Fig. 2 Map showing location of Hidaka province (above) and of localities where samples were obtained.

Figures represent towns or villages visited for blood sample collection. For key see table 1.

The coastal distance from Samani to near the Iburi border is approximately 64 miles.

Osachinai (30) is approximately 18 miles inland along the Sarugawa.

Each hamlet or village formerly consisted of 20 to 30 houses and 3 to 5 villages made a small district. Consanguineous marriage was the custom, with the result that Ainus from a particular district show very similar physical characteristics.

Table 2 shows the number of districts represented in the three series for Ainu and Ainu-Japanese.

Table 3 shows the sex distribution and numbers for each of the three series in the survey. The majority tested were over 21 years of age.

TABLE 1

Towns visited in Hidaka for blood sample collection Island of Hokkaido. (See figure 2)

Series I	Samani (1), Okada (2), Kineusu (3), Nishicha (4), Ikantai (5), Anecha (6), Nobuka (7).
Series II	Utafue (8), Hōei (9), Tomisawa (10), Nishi-Hōrai (11), Showa (12), Kamimori (13), Noya (14).
Series III	Takae (15), Saruwarabe (16), Mihara (17), Ukegoi (18), Motokanbe (19), Fukumitsu (20), Shiunkotsu (21), Sarba (22), Nina (23), Piratori (24), Nibutani (25), Penakore (26), Nioi (27), Nioi-Honson (28), Nukkibetsu (29), Osachinai (30).

RESULTS AND DISCUSSION

The A-B-O groups and subgroups. Table 4 presents the results of the A-B-O grouping of 271 Ainu and 159 Ainu-Japanese together with calculated gene frequencies. In the Ainu $p = .285$, $q = .212$, $r = .512$ and in Ainu-Japanese $p = .236$, $q = .203$, $r = .549$. The outstanding feature in the table is the variation seen in q, the gene for group B. In series I and series II the q figure for both Ainu and Ainu-Japanese was low and r was high compared with series III. This suggested that the population from which the series were drawn was not homogeneous and one of us (S.K.) supplied the following comments on this point. The Ainus of the three series have some different customs; for example, the design of the tattooing of women is different. Anthro-

pologically the difference between series III and series II was larger than between series II and series I. The Hidaka province could well be divided into two anthropological districts, namely East Hidaka (from Shizunai to Samani) and West Hidaka (from the Iburi border to Shizunai). The former corresponds with series I and II, and the latter with series III.

TABLE 2

Number of districts in Hidaka represented by blood samples

POPULATION	SERIES I	SERIES II	SERIES III
Ainu	14	17	26
Ainu-Japanese	13	21	23

Seven districts in Series II were common to Series I.
Two districts in Series II were common to Series III.

TABLE 3

Sex distribution and numbers

SERIES	AINU			AINU-JAPANESE			NUMBER UNDER 21 YEARS OF AGE
	Total	Males	Females	Total	Males	Females	
I	79	33	46	21	13	8	12
II	80	20	60	75	30	45	22
III	112	43	69	63	29	34	22
Totals	271	96	175	159	72	87	56

The differences in q frequencies which appear in the Ainu surveys for different localities tabulated by Boyd ('39) are referred to later in the text when p, q, r comparisons shown in table 10 for Ainu, Japanese and Ainu-Japanese are discussed.

The subgroups of A. Tests for the A_1-A_2 subgroups showed that in Ainu 101 persons of group A and 28 of group AB, and in Ainu-Japanese 50 of group A and 19 of group AB were all of subgroup A_1 and A_1B respectively.

The M-N types and S subdivisions. Table 5 presents the results of M-N tests in 265 Ainu and 158 Ainu-Japanese with

anti-S tests in 257 and 157 respectively. The gene frequencies found were $m = .396$ and $n = .604$ for Ainu; and $m = .418$ and $n = .582$ for Ainu-Japanese.

TABLE 4

The A-B-O blood groups and gene frequencies

SERIES	NUMBER OF BLOOD SAMPLES TESTED	BLOOD GROUPS				GENE FREQUENCIES		
		O	A_1	B	A_1B	p	q	r
AINU								
I	79	29	38	9	3	.315	.088	.606
		37 %	*48 %*	*11 %*	*4 %*			
II	80	27	34	18	1	.292	.169	.581
		34 %	*42.5%*	*22.5%*	*1 %*			
III	112	15	29	44	24	.261	.360	.366
		13.4%	*25.9%*	*39.3%*	*21.4%*			
Totals	271	71	101	71	28	.285	.212	.512
		26.2%	*37.3%*	*26.2%*	*10.3%*			
AINU-JAPANESE								
I	21	7	7	4	3			
II	75	28	27	14	6	.245	.137	.611
		37 %	*36 %*	*19 %*	*8 %*			
III	63	13	16	24	10	.224	.312	.454
		21 %	*25 %*	*38 %*	*16 %*			
Totals	159	48	50	42	19	.236	.203	.549
		30.2%	*31.4%*	*26.4%*	*11.9%*			
COMBINED RESULTS								
Totals	430	119	151	113	47	.266	.208	.526
		27.7%	*35.1%*	*26.3%*	*10.9%*			

Again series III differed from series I and II and this applied in both Ainu and Ainu-Japanese. In both groups ("pure" and mixed) series I and II showed a higher m frequency than did series III. These differences in m and n frequencies are discussed later in relation to table 11, which compares them with the results of an earlier M-N survey in Ainu, and a similar survey in Japanese at Sapporo. Of

257 Ainu samples 123 (47.9%) were S positive and of 157 Ainu-Japanese 71 (45.2%) were S positive.

Approximate chromosomal frequencies:

Ainu: $ms = .385$; $mS = .012$; $ns = .326$; $nS = .277$.
Ainu-Japanese: $ms = .387$; $mS = .030$; $ns = .356$; $nS = .227$.

In a paper by Graydon, Simmons, Semple, Clapham, Wallace and Harrisson ('52) a table is given showing the S distribution for various races tested to date. The Ainu figures $mS = .012$ and $nS = .277$ are not like those of any other race. Australian aborigines have little or no S antigen. In Australian whites $mS = .261$ and $nS = .069$, figures very similar to those published for English individuals. Unfortunately the S distribution in Japanese has not yet been investigated.

M or N variants. A total of 130 random blood samples were tested with two anti-M and two anti-N sera. No M or N variants were detected.

The Rh types and gene frequencies. Table 6 presents the Rh types and gene frequencies found in 257 Ainu and in 157 Ainu-Japanese. The calculated gene frequencies were:

$R^1 = .556$; $R^2 = .210$; $r'' = .197$; $R^o + r = .037$ for Ainu, and $R^1 = .553$; $R^2 = .227$; $r'' = .135$; $R^o + r = .065$; $r' = .020$ for Ainu-Japanese.

From the results of the Rh surveys on Japanese resident in U. S. A. (New York and Denver) made by Waller and Levine ('44) who tested 150 persons, and Miller and Taguchi ('45) who tested 180 persons, and from those of Chown et al. ('46) who tested 217 unrelated persons of Japanese origin in Canada, the following gene frequencies are presented together with those for 157 Ainu-Japanese.

	R^1	R^2	R^z	r	r'	r''
Japanese						
150 tested	.60	.37	0	.02	.005	.005
180 tested	.702	.277	0	.021	0	0
217 tested	.580	.307	.004	.080	0	.029
Ainu-Japanese						
				$R^o + r$		
157 tested	.553	.227	0	.065	.020	.135

The M-N types, S distribution and gene frequencies

SERIES	NUMBER OF BLOOD SAMPLES TESTED	M-N TYPES M	MN	N	FREQUENCY OF GENES *m*	*n*	PROPORTION OF SAMPLES S POSITIVE	DISTRIBUTION OF S POSITIVE CELLS M	MN	N
AINU										
I	79	14 *18 %*	40 *51 %*	25 *32 %*	.430	.570	46/79 *58 %*	2/14	20/40	24/25
II	80	16 *20 %*	36 *45 %*	28 *35 %*	.425	.575	35/80 *44 %*	1/16	14/36	20/28
III	106	14 *13.2%*	46 *43.4%*	46 *43.4%*	.349	.651	42/98 *43 %*	0/13	18/42	24/43
Totals	265	44 *16.6%*	122 *46.0%*	99 *37.4%*	.396	.604	123/257 *47.9%*	3/43 *7%*	52/118 *44.1%*	68/96 *71%*
AINU-JAPANESE										
I	21	6	10	5	.52	.48	7/21	1/6	3/10	3/5
II	75	14 *19 %*	33 *44 %*	28 *37 %*	.407	.593	38/75 *51 %*	2/14	16/33	20/28
III	62	13 *21 %*	23 *37 %*	26 *42 %*	.395	.605	26/61 *43 %*	3/13	9/22	14/26
Totals	158	33 *20.9%*	66 *41.8%*	59 *37.3%*	.418	.582	71/157 *45.2%*	6/33 *18%*	28/65 *43%*	37/59 *63%*
COMBINED RESULTS										
Totals	423	77 *18.2%*	188 *44.4%*	158 *37.4%*	.404	.596	194/414 *46.9%*	9/76 *11%*	80/183 *44%*	105/155 *68%*

Approximate chromosomal frequencies calculated from the figures in the present survey are as follows:

Ainu	*ms* .385;	*mS* .012;	*ns* .326;	*nS* .277.
Ainu-Japanese	*ms* .387;	*mS* .030;	*ns* .356;	*nS* .227.
Combined results	*ms* .385;	*mS* .020;	*ns* .338;	*nS* .257.

TABLE 6

The Rh types and gene frequencies

SERIES	NUMBER OF BLOOD SAMPLES TESTED	RH TYPES								
		Rh_1Rh_1	Rh_1rh	Rh_2Rh_2	Rh_2rh	Rh_1Rh_2	Rh_o	rh″rh″	rh″rh	rh′rh″
AINU										
I	79	26 *33 %*	5 *6 %*	12 *15 %*	0	34 *43 %*	0	1 *1 %*	1 *1 %*	0
II	80	29 *36 %*	6 *7.5%*	8 *10 %*	2 *2.5%*	29 *36 %*	0	4 *5 %*	2 *2.5%*	0
III	98	28 *29 %*	1 *1 %*	16 *16 %*	2 *2 %*	45 *46 %*	0	6 *6 %*	0	0
Totals	257	83 *32.3%*	12 *4.7%*	36 *14.0%*	4 *1.6%*	108 *42.0%*	0	11 *4.3%*	3 *1.2%*	0
AINU-JAPANESE										
I	21	7	0	4	0	9	1	0	0	0
II	75	27 *36 %*	11 *15 %*	9 *12 %*	1 *1 %*	26 *35 %*	0	1 *1 %*	0	0
III	61	21 *34 %*	1 *2 %*	6 *10 %*	0	30 *49 %*	0	2 *3 %*	0	1 *2 %*
Totals	157	55 *35 %*	12 *7.6%*	19 *12.1%*	1 *.6%*	65 *41.4%*	1 *.6%*	3 *1.9%*	0	1 *.6%*
COMBINED RESULTS										
Totals	414	138 *33.3%*	24 *5.8%*	55 *13.3%*	5 *1.2%*	173 *41.8%*	1 *.2%*	14 *3.4%*	3 *.7%*	1 *.2%*

There is indeed a similarity in the Rh genes found and in the gene frequencies for Japanese and Ainu-Japanese.

The outstanding features of the present Rh survey in Ainu and Ainu-Japanese were:

1. The high r'' gene frequency, .197, which is by far the highest yet reported for any race.

2. Tests with an anti-rh″ (anti-e) serum showed that in Ainu 4.3% were rh″rh″ and 1.2% were rh″rh, thus the presence of the rh negative gene r was unequivocally demonstrated. The 17 cells typed as rh″ were subjected to tests with a large selection of potent anti-D and anti-D + D^u agglutinating sera, as well as with a number of potent anti-C sera. We are satisfied that the cells so classified have no Rh_o (D), or rh′ (C) agglutinating content.

3. Type Rh_o was not detected in Ainu but was demonstrated in one Ainu-Japanese.

The finding of 5.5% rh″ in Ainu (as well as the unique S distribution in the M-N types) places the Ainu in a category apart from other aboriginal races. Simmons and Graydon ('48) demonstrated the presence of 1.7% rh′rh′ in 234 Australian aborigines but no rh″. The latter group also contained 3% Rh_1Rh_z. The gene R^z was not detected in Ainu.

The cross-over theory. The Rh figures of this survey lend no support to Fisher's cross-over theory (Fisher and Race, '46) by which he suggested that the frequencies of the rarer Rh types might be maintained by crossing over of gene elements in chromosomes of the more commonly occurring heterozygotes to form the rarer chromosomal arrangements. In a previous paper (Simmons and Graydon, '48) attention was drawn to the lack of confirmation of this theory in the results of Rh typing of Australian aborigines.

Crossing-over effects are possible only in those who are heterozygous for more than one gene element. In the Ainu the most common double heterozygote is R^1R^2(CDe/cDE) which by crossing over can produce only R^o(cDe) and R^z-(CDE) in equal proportions. The gene R^z was not found in

the Ainu or in the Ainu-Japanese but R^o was shown to exist in the latter.

The only heterozygote found which could produce r''(cdE) is R^2r(cDE/cde) and this would also produce R^o(cDe). However the frequency of r'' in the Ainu is at least 6 times that of R^o and it is also much greater than the frequency of R^2r, its possible progenitor.

There is also the triple heterozygote R^1r''(CDe/cdE) which could cross over in three different ways, producing R^o(cDe) and r^y(CdE), r'(Cde) and R^2(cDE), and R^z(CDE) and r(cde). There is no evidence to suggest that any of these cross-overs has occurred. Genes r^y and R^z were not detected in the series.

Most certainly then, crossing over could not account for the high frequency of r'' in the Ainu and it is felt that the only plausible assumption is that the Ainu originally had a high frequency of r'', possibly the highest in the world. In view of their racial antiquity it is tempting to suggest that this race or one of its major components may have been the primary source from which the r'' gene was disseminated to other races possessing this gene, throughout the world.

Tests for the $Rh_o(D^u)$ variants. Fifty random blood samples were tested with 5 known anti-D and anti-D + D^u sera. No example of Stratton's D^u was detected.

Tests for the C^w variant. A total of 268 Ainu and 157 Ainu-Japanese blood samples were tested with a potent anti-C^w agglutinating serum found in Melbourne. No C^w variant was detected.

The Lewis (Le^a) blood group. Of 227 Ainu, and 111 Ainu-Japanese blood samples tested with anti-Le^a serum; 34.4% and 36.9% respectively were Le(a +). The results for Ainu show a progressive increase in Le(a +) percentage in the areas defined by series I, II and III respectively. The same trend appears in the smaller Ainu-Japanese series.

The correlation between the Le^a blood group and A, B or H secretion in saliva. A total of 91 corresponding blood and saliva samples from Ainu were tested for the Le^a blood group and A-B or H salivary secretion. Twenty-five per cent

were Le(a +), ss; 65% were Le(a —), S and 10% were Le(a —), ss; that is, in 10%, correlation was not obtained. In a paper dealing with Marshallese, Simmons et al. ('52) have given 4 possible reasons which may explain why such exceptions were found in this type of survey. It will be noticed

TABLE 7

The Lewis blood group

AINU

SERIES	NUMBER OF BLOOD SAMPLES TESTED	Le (a+)	Le (a–)
I	35	8 *23 %*	27 *77 %*
II	80	24 *30 %*	56 *70 %*
III	112	46 *41.1%*	66 *58.9%*
Totals	227	78 *34.4%*	149 *65.6%*
AINU-JAPANESE			
I	13	5	8
II	75	24 *32 %*	51 *68 %*
III	23	12	11
Totals	111	41 *36.9%*	70 *63.1%*
COMBINED RESULTS			
Totals	338	119 *35.2%*	219 *64.8%*

that S in this case represents A, B or H secretion, and ss represents non-secretion. The use of the same letters, S and s, for denoting the A, B, H salivary secretion genes and the S subdivisions of the M-N system which are unrelated, can be very confusing particularly to those who are not actually engaged in blood grouping, and it is hoped that the nomen-

clatures of these two independent systems will receive early attention from an internationally accredited committee.

In Ainu-Japanese in a total of 63 corresponding tests, 43% were Le(a +), ss; 56% were Le(a —), S; and 2% were Le(a —), ss. That is, failure to obtain correlation occurred only once in 63 corresponding samples. The number tested for correlation was less than planned, due to the accident

TABLE 8

Correlation of Lewis blood group and A, B or H secretion in saliva

SERIES	NUMBER OF SUBJECTS TESTED	Le (a+) ss	Le (a–) S	Le (a–) ss
AINU				
I	34	7	25	2
II	39	12	13	4
III	18	4	11	3
Totals	91	23	59	9
		25 %	*65 %*	*10 %*
AINU-JAPANESE				
I	13	5	8	0
II	28	10	17	1
III	22	12	10	0
Totals	63	27	35	1
		43 %	*56 %*	*2 %*
COMBINED RESULTS				
Totals	154	50	94	10
		32.5%	*61 %*	*6.5%*

which caused haemolysis of the original series II blood samples, and to some jars of saliva with faulty screw caps.

The Lewis blood tests and tests for salivary secretion were performed by workers independently in two separate laboratories and the results were compared only at the conclusion of the tests.

Table 9 shows the A, B or H secretion in 229 saliva samples in Ainu and Ainu-Japanese. There were 145 (63.3%) secre-

tors and 84 (36.7%) non-secretors. These may be compared with the Le^a blood group (table 7), in which the combined results for 338 Ainu and Ainu-Japanese were Le(a —) 64.8% and Le(a +) 35.2%. The figures show particularly that suitably preserved blood samples from the field can be Lewis tested with a high degree of accuracy. It has been claimed that the Lewis, and certain other blood antigens disappear rapidly in blood samples collected for anthropological surveys, but this has not been our experience. The explanation of these discrepancies probably lies in different methods of collecting and testing samples.

The blood group P. One hundred Ainu blood samples of the repeated series II were tested with an anti-P serum at

TABLE 9

A-B or H secretion in 229 saliva samples

AINU AND AINU-JAPANESE

O		A_1		B		A_1B		TOTALS	
S	ss	S	ss	S	ss	S	ss	S	ss
50	27	57	35	28	18	10	4	145	84
65%		*62%*		*61%*		*71%*		*63.3%*	*36.7%*

5°C., and readings were made at the same temperature. Of these, 72% were regarded as P positive. Twenty-three samples gave good positive reactions, 49 were recorded as weakly positive, and 28 were classed as negative. Difficulties in reading P results seem to have been experienced by most workers. Our main difficulty is due to the fact that the anti-P serum available to us is not comparable in potency with other testing sera selected for these surveys. In many instances a decision between weak P-positive or P-negative is difficult to make.

The Duffy and Kell blood groups. Only limited tests for the Duffy and Kell blood groups were performed because of short supplies of testing sera. When sera became available to us the original Ainu samples had been stored at 5°C. for

10 months. Later, we were also able to test samples which were only 10–14 days old.

In Ainu, no great difference in Duffy results was found between samples 14 days old and 10 months old. In all, 27 Ainu samples were tested and of these, 26 were Duffy positive (96%). In Ainu-Japanese, 24/24 (100%) were Duffy positive. Thus is can be predicted that "pure" Japanese like many other Pacific races will prove to be about 100% Duffy positive.

The Kell tests were also done on the same two lots of blood samples. In Ainu, 4/27 (15%) were regarded as Kell positive, and in Ainu-Japanese, 2/24 (8%) were recorded as positive. It should be stated that in earlier Kell tests we were worried by the occurrence of some non-specific reactions as distinct from clear-cut positive reactions. All the Duffy and Kell tests were made by the indirect Coombs test as the test sera were both of the blocking, or incomplete type. The Kell results are presented with a little reserve, but it is thought that they give a fairly true picture. Three anti-Kell sera were used in testing 24 samples 10–14 days old. Two clear-cut positives with all three sera were found. Some difference of opinion appears to exist regarding the stability of Kell antigen. In personal communications we have been advised that Kell antigen disappears in possibly 24 hours from whole blood samples sent through the post, whereas others have not found it so unstable. To test the stability of the Kell antigen under our conditions we selected 12 blood samples from persons of known blood types on our panel. The samples had been stored in glucose-citrate preserving solution at 5°C. for periods from 5 days to 20 months. All samples were Rh typed and tested for the Duffy and Kell blood groups as unknowns. The Rh, Kell and Duffy tests were entirely satisfactory, and the results obtained were identical with those obtained with freshly collected cells. From these and other tests we have reached the conclusion that most of the blood group antigens of suitably preserved cells deteriorate at much the same rate. In tests with potent sera this de-

terioration is usually unimportant, but when the sera are weak it may seriously affect the accuracy of the results.

The cell suspending medium, asepsis, and temperature of storage are each important in keeping this deterioration to a minimum.

Taste reactions to phenyl-thiocarbamide. In Ainu, 70 (21.3%) were recorded as tasters, 237 (72.3%) as weak tasters and 21 (6.4%) as non-tasters. In Ainu-Japanese the figures were 34 (19.4%) tasters, 132 (75.4%) weak-tasters and 9 (5.1%) non-tasters.

The difficulties in obtaining a completely reliable picture of taste reactions are generally recognized. The results obtained can often be regarded as no more than an approximate indication of ability to taste. One of us (S.K.) who carried out the tests does not regard the Ainu results as completely trustworthy in spite of careful efforts in the field. The Ainu do not have bitter substances in their diet or in their local medicines, and therefore this factor has not influenced the results. They were not regarded as particularly sensitive to the PTC test although a high percentage of tasters was recorded. A high percentage of tasters was also recorded in Maoris by Simmons et al. ('51).

Ainu and Japanese: p, q, r frequencies. Table 10 shows comparative p, q, r frequencies for Ainu and Japanese of Hokkaido. As stated earlier in the text the Ainu surveys tabulated by Boyd ('39) show a marked locality difference in values of q, the gene for group B, and r, the gene for group O, while p remains fairly constant. Thus at Piratori (249 tested) $q = .335$ and at the adjacent town or village of Nibutani $q = .388$ (only 50 tested). A little further east at Shizunai q was .111 for 504 tested, a marked drop in frequency. In the present survey similar differences were revealed. Thus, for the area from Samani to Shizunai (series I and II) q was .129 and r was .593 but for series III, towns and villages mostly along the Iburi border and including Piratori and Nibutani, q was 0.360 and r was .366. The q figure of .360 for this area which includes the towns of Piratori and Nibu-

tani indicates an area (as distinct from any one small group) with possibly the highest q frequency in the world, reported to date. The present results therefore agree with those recorded for earlier surveys and show that the values of q and

TABLE 10

Comparative p, q, r gene frequencies

AINU AND JAPANESE: HOKKAIDO

POPULATION	LOCALITY	AUTHORS	NUMBER TESTED	GENE FREQUENCIES		
				p	q	r
Ainu	Piratori (Hidaka)	Grove [1]	249	.299	.335	.341
Ainu	Nibutani (Hidaka)	Ninomiya [1]	50	.317	.388	.346
Ainu	Shizunai (Hidaka)	Kubo [1]	504	.295	.111	.606
Japanese	Hokkaido	Furuhata [1]	5360	.259	.173	.564
Ainu	Series I, II (Hidaka)	Present survey	159	.304	.129	.593
	Series III [2] (Hidaka)		112	.261	.360	.366
	Series I, II, III [3] (Hidaka)		271	.285	.212	.512
Ainu-Japanese	Series I, II	Present survey	96	.244	.139	.604
	Series III		63	.224	.312	.454
	Series I, II, III		159	.236	.203	.549
Ainu + Ainu-Japanese (Total)	Series I, II	Present survey	255	.282	.133	.597
	Series III		175	.246	.341	.400
	Series I, II, III		430	.266	.208	.526

[1] Cited by Boyd ('39).
[2] Series III locality includes Piratori and Nibutani.
[3] Series I, II, III collected in 30 towns or villages.

the values of r vary considerably from area to area within the province. The frequencies found for 271 Ainu over the larger area covered in this survey probably give a better picture of Ainu frequencies, and were $p = .285$, $q = .212$, $r = .512$.

The same local variation in frequencies is reflected in the results for Ainu-Japanese given in table 10.

The p, q, r frequencies for 5360 Japanese of Hokkaido are $p = .259$, $q = .173$, $r = .564$ and are typical of the results for numerous surveys conducted in various parts of Japan. They differ little from the total Ainu frequencies obtained in the present survey.

TABLE 11

Comparative m and n gene frequencies

AINU AND JAPANESE: HOKKAIDO

POPULATION	LOCALITY	AUTHORS	NUMBER TESTED	GENE FREQUENCIES	
				m	*n*
Ainu	Shizunai [3] (Hidaka)	Kubo [1]	504	.430	.570
Japanese	Sapporo (Ishikari)	Yamanaka [1]	562	.553	.447
Ainu	Series I, II	Present survey [2]	159	.428	.572
	Series III		106	.349	.651
	Series I, II, III		265	.396	.604
Ainu-Japanese	Series I, II	Present survey	96	.432	.568
	Series III		62	.395	.605
	Series I, II, III		158	.418	.582
Ainu and Ainu-Japanese (combined)	Series I, II	Present survey	255	.429	.571
	Series III		168	.366	.634
	Series I, II, III		423	.404	.596

[1] Cited by Boyd ('39).
[2] Series I, II, III collected in 30 towns or villages.
[3] Shizunai in Series I and II area.

Ainu and Japanese: m, n frequencies. Further comparisons using the M-N blood group system are given in table 11. Some evidence of locality variation is again seen when the M-N frequencies for series I and II are compared with series III, both for Ainu and Ainu-Japanese. An earlier Ainu survey at Shizunai showed $m = .430$ and $n = .570$, and these frequencies are almost identical with those of the pres-

ent series I and II ($m = .428$ and $n = .572$). Series III frequencies (mostly near the Iburi border) show a decrease in m and a corresponding increase in n, thus $m = .349$ and $n = .651$.

The frequencies found for 265 Ainu over the entire area of the present survey are $m = .396$ and $n = .604$ and these are probably representative of the Hidaka Ainu today. The 562 Japanese tested at Sapporo show frequencies, $m = .553$, $n = .447$, which are typical of some 14 surveys in Japan including the more recent survey on 400 reported by Graydon et al. ('45) who found $m = .540$, $n = .460$.

A direct comparison of the m and n frequencies for Ainu, Ainu-Japanese and Japanese is as follows:

		m	n
Ainu	(265)	.396	.604
Ainu-Japanese	(158)	.418	.582
Combined results	(423)	.404	.596
Japanese	(562)	.553	447

If a blending of the Japanese and Ainu races has taken place in past centuries as the similarity in A-B-O groups and Rh types seems to suggest, the original m frequency for Japanese may have been greater than .6 as in Chinese and Siamese and the m frequency in Ainu may well have been less than .3 as in Australian aborigines, Papuans and New Caledonians.

The secretor types in Ainu and Japanese. Two surveys on Japanese have been cited in a table of secretor types prepared by Simmons, Semple and Graydon ('51). New unpublished data for various Pacific populations show that in a number of races, including the Australian aborigines, 90–100% are A, B or H secretors (S).

The two Japanese surveys referred to show 75.7% and 79.5% secretors respectively. In the present survey 65.6% of 227 Ainu were Le(a —) and these with few exceptions would be secretors. In 111 Ainu-Japanese 63.1% were Le-(a —). Of those individuals whose cells were tested for

the Le^a blood group and whose saliva was also tested (table 8) 65% of 91 Ainu were secretors and 56% of 63 Ainu-Japanese were secretors. (The lower figures for Ainu-Japanese are probably due to locality or chance variation.) In all, 229 salivas for both Ainu and Ainu-Japanese were tested and it was found that 63.3% were secretors of the A, B or H substances. It is recognized that the procedure which involved collection and rapid boiling of saliva samples in the field and their transport through the tropics to a distant center was not completely satisfactory. However, the figure of 65% secretors for Ainu is probably fairly accurate. Although the secretor figures reported for Japanese are 75-80% the difference in figures for the two races is not extreme. Again it may be asked if this is further evidence of a blending of the races. The Le(a +) percentage of 34.4 in blood is the highest for any race tested to date by us. Thus if blending has occurred one may assume that the original Ainu figure was still higher. That is, the original Ainu salivary secretor percentage was most likely less than the 65% found in the present survey.

The Ainu, Australian aborigines and American Indians. Anthropologists have suggested on purely physical grounds a relationship between Ainu, Australian aborigines and possibly American Indians. In an attempt to equate genetically these three races the search for common components is hampered by alteration of physical characteristics by other admixture. Trouble from this source is of less significance in the case of blood groups because of their specificity and the lack of interaction between genes of the various blood group systems. Blood genes possessed in appreciable frequency by any common component should be demonstrable in the blood of each of these three peoples. This approach is limited, however, by the occurrence of many of the blood group genes in various proportions in all human races.

Suppose then the postulated racial mixture for each population is examined to see what blood factors must have been originally present or lacking in the common component,

as shown by the blood grouping data available today. The comparative gene frequencies are given in table 12. The possible physical components discussed by Birdsell ('51 a and b) are as follows:

Ainu = Ainu (proto-Caucasian) and Mongoloid. Australian aborigines = (a) a single homogeneous race (Abbie, '51, and others) or (b) Negrito, Murrayian (proto-Caucasian) and Carpentarian. American Indians = Mongoloid and Amurian.

Group B. If an Ainu component as suggested is the same as the Murrayian component of Australian aborigines (both described as proto-Caucasian), and is also closely related to the Amurian component of American Indians (a population according to Birdsell as ancestral to living Ainu and Murrayians), then the original common component must have lacked group B (gene q) or possessed it only in very low frequency, because it is absent in Australian aborigines and American Indians. If group B in the present Ainu was derived from Mongoloid admixture it is remarkable that in areas of Hidaka q is possibly the highest in the world. Further the total of 271 "pure" Ainu collected over a large area of Hidaka show $q = .212$, while q for Japanese in Sapporo was .173; a figure typical of numerous surveys throughout Japan. The absence of group B from Australian aborigines and American Indians means, further, that it was absent from, or occurred rarely in all postulated components for these peoples.

The S subdivision of M-N. Figures for the S subdivision of the M-N types show that S is absent in Australian aborigines (therefore in all three postulated components), but occurs in 48% of Ainu blood samples. No S figures for American Indians have been seen by us to date. We have no S percentage for Japanese as yet, but it might be assumed that the Japanese and Chinese S figures would be somewhat comparable. Miller, Rosenfield and Vogel ('51) have reported that 10.7% of 103 Chinese in U. S. A. were anti-S positive. If the Japanese S percentage is similar, then it

becomes difficult to attribute this high S percentage in Ainu to Mongoloid mixture, when the frequency is probably higher than the Mongoloid people themselves possess. Thus, as the position is similar in relation to the two blood factors B and S, it would appear that an original Ainu component possessed a higher percentage of both factors than the Mongoloid component with which they subsequently mixed. (Dr. A. E. Mourant has informed us that the S antigen has been demonstrated in 46% of Navaho Indians.)

Type Rh_o. Little can be said about the blood factor Rh_o as it may or may not be present in low frequency in Ainu, and its calculated frequency in Australian aborigines and American Indians is very low.

Type Rh_z. The blood factor Rh_z has been shown to be present in both Australian aborigines and American Indians but was not demonstrated in the present Ainu survey. It has been demonstrated in Mongoloid people and other peoples of the Pacific by some of the present authors. In American Indians it may be thought to be due to the Mongoloid element which strangely must have lacked group B, but in Australian aborigines its presence is not easily explained. In American Indians and Australian aborigines its percentage is the highest yet reported. Both may have derived it from a common source but that source does not appear to be also an Ainu component.

Type rh. The rh negative gene *r* was unequivocally demonstrated associated with *r″* in Ainu, by the use of anti-rh″ (anti-e) serum. It has not been detected in Australian aborigines or in "pure" American Indians. Its presence in Ainu can hardly be attributed to Mongoloid admixture, as it has not been detected in several surveys on selected samples from Mongoloid peoples in their own country, but has been found in Japanese and Chinese resident in U. S. A. in low frequency. It must be accepted then, that an Ainu component (not Mongoloid) possessed this gene; but did not convey it to the Australian aborigines or American Indians.

Type rh′. In Ainus and American Indians rh′ has not been demonstrated, whereas it was found in 1.7% of a sampling of Australian aborigines with a calculated gene frequency for *r′* of .129. Unpublished observations on the Chenchus of India show that they possess rh′, and this may be taken to support the suggestion of an Australian link with India, and further, to support a proto-Caucasian origin for Australians because Caucasians also possess this gene. Few colored people to date have been shown to possess rh′.

Type rh″. The blood factor rh″ is of the greatest interest because it was detected in 5.5% of the Ainu over the full area of the survey. The Ainu are thus outstandingly rich in a gene which had been found virtually only in the white race, and then in low frequency. Type rh″ has, however, been demonstrated in two surveys on Japanese. Perhaps the postulated proto-Caucasian component of the Ainu contributed this gene to the white race. The blood factor has not been detected in either Australian aborigines or American Indians and again a common component might have been expected to have carried it to them.

Type Le^a and secretor, S. In Ainu 34.4% were Le(a +) with 65% secretors and in recent unpublished work on Australian aborigines the Le(a +) percentage was approximately 6, with 97% secretors. The American Indian figure for Le(a +) is not known by us but as judged by the reports on them for the secretor factor it should be zero. In Japanese 75–80% have been shown to be secretors and by inference 20–25% should be Le(a +). The Ainu therefore possess a higher Le(a +) per cent than the Mongoloid people, and thus the high percentage for Ainu cannot be attributed to Mongoloid admixture.

Type Fy^a. The Duffy blood type (Fy^a) was present in 96% of the Ainu tested, and in 100% of Ainu-Japanese. In Australian aborigines tested to date, the percentage is 100. Pantin and Junqueira ('51) reported Fy^a to be absent in 73 pure Brazilian Indians. Comment on the Duffy factor

TABLE 12

Comparative gene frequencies in Ainu, Australian aborigines and American Indians

POPULATION	p	q	r	m	n	S POSITIVE %	R^0	R^1	R^2	R^z	r (R^0+r)	r'	r''	Le (a+)	SECRETOR (S)	DUFFY [1] (Fy^a)	KELL (K)	P+	P.T.C. TASTERS
Ainu	.285	.212	.512	.396	.604	47.9%	..	.556	.210	0	.037	0	.197	34.4%	65%	96%	15%	72%	93.6%
Australian aborigines	.251	0	.749	.297	.703	0	.085	.564	.201	.021	0	.129	0	6 %	97%	100%	0	67%	50 %
American Indians (Ute)	.011	0	.989	.76	.24	..	?	.524	.476	0	0	0	0	[2]	100%	..	..	..	..
(Mexico)	031	.016	.953	.79	.21	..	.06	.64	.27	.03	0	0	0	..	..	..	..	..	..

[1] Pantin and Junqueira ('52) found 73 Brazilian Indians to lack the Duffy (Fy^a) factor.

[2] This group could be presumed to lack the Lewis (Le^a) factor because they were 100% secretors.

should await the reports of investigations on Indian populations in North America.

HAIRINESS OF AINU AND AUSTRALIAN ABORIGINES

A comparison has often been made between Ainu and Australian aborigines because each race possesses a high degree of hairiness. There is no evidence that genes for hairiness are related to the blood group genes, but it is possible that the same common component contributed genes for hairiness and certain blood groups to both races. This would seem to be further evidence against an identical component occurring in the American Indians.

Having considered separately the blood factors B, S of M-N, Rh_o, Rh_z, rh, rh′, rh″, Le^a and secretor (S) in relation to Ainu, Australian aborigines and American Indians, it is considered that the genetic evidence is against a postulated proto-Caucasian component common to all three peoples.

Both Ainu and Australian aborigines individually possess certain genes present, or rare, in Caucasians. For example, Ainus possess *r* and *r″*, the Australian aborigines possess R^o, R^z and *r′*, while American Indians lack *r*, *r′* and *r″* but possess R^z. Most other colored races lack *r*, *r′* and *r″*, although *r* and *r′* have been demonstrated in some Asian Indians. If the presence of factors *r*, *r′* and *r″* are considered sufficient to indicate a Caucasian link, then there is some evidence that Ainu and Australian aborigines each possess a proto-Caucasian component, but not necessarily the same one. The suggested proto-Caucasian component in Australian aborigines and some people of South India may be the same, if the common possession of *r′* in easily demonstrable quantities, is significant.

Birdsell ('51a) has discussed at length, and favors, a trihybrid origin for Australian aborigines. For his views to be genetically tenable it will be noted that all three postulated components must lack the blood factors B, S of M-N, rh, rh″ and possibly Kell. The details of recent blood work on Australian aborigines will be published at a later date.

It is realized that the above discussion though based on data more extensive than was previously available, is itself far from complete and may well be interpreted differently by others. The main purpose of the investigation has been achieved, the placing on record of new genetic data for the Ainu before that population disappears as an entity.

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SUMMARY

1. Eight genetic characters in Ainu and Ainu-Japanese have been studied and calculated gene frequencies presented.

2. In 271 Ainu: $p = .285$, $q = .212$, $r = .512$. In 159 Ainu-Japanese: $p = .236$, $q = .203$, $r = .549$. In the three series of Ainu tested the values of q were .088, .169, .360. In one area q is possibly the highest recorded to date. The values of q and r are variable within the province, the present results agreeing with those of earlier surveys. Tests for the A_1-A_2 subgroups showed that in Ainu 101 persons of group A and 28 of group AB, in Ainu-Japanese 50 of group A and 19 of group AB were all subgroups A_1 and A_1B respectively.

3. In 265 Ainu: $m = .396$, $n = .604$. In 158 Ainu-Japanese: $m = .418$, $n = .582$. Variations in m and n within the province correspond to those found in q and r. A total of 130 random blood samples was tested for M or N variants. No variants were detected. In Ainu: 123/257 (47.9%) were anti-S positive. In Ainu-Japanese: 71/157 (45.2%) were anti-S positive.

The calculated chromosomal frequencies were:

Ainu:	$ms = .385$; $mS = .012$; $ns = .326$; $nS = .277$.
Ainu-Japanese:	$ms = .387$; $mS = .030$; $ns = .356$; $nS = .227$.

The S distribution has no counterpart in any other race tested to date.

4. The calculated Rh frequencies in 257 Ainu and 157 Ainu-Japanese were:

Ainu:	$R^1 = .556$; $R^2 = .210$; $r'' = .197$; $R^o + r = .037$.
Ainu-Japanese:	$R^1 = .553$; $R^2 = .227$; $r'' = .135$; $R^o + r = .065$; $r' = .020$.

The Ainu have much the highest frequency yet found of gene r'', which previously had been discovered only in the

white peoples. This suggests that their proto-Caucasian component may have been the original source of this gene. The Rh negative gene *r* associated with *r''* was demonstrated unequivocally. Both genes occur in Caucasians. Fifty random blood samples were tested with 5 known anti-D and anti-D + D^u sera. No example of Stratton's D^u was detected.

A total of 268 Ainu and 157 Ainu-Japanese blood samples were tested with a potent anti-rh^w (anti-C^w) agglutinating serum. No $rh^w(C^w)$ variant was detected.

5. A total of 227 Ainu, and 111 Ainu-Japanese blood samples were tested with anti-Le^a serum, and 34.4% and 36.9% were Le(a +) respectively.

A total of 91 corresponding blood and saliva samples from Ainu were tested for the Le^a blood group and A, B or H salivary secretion; 25% were Le(a +), ss; 65% were Le(a —), S; and 10% were Le(a —), ss. Thus, failure to obtain correlation occurred in 10%. In 63 Ainu-Japanese 43% were Le(a +), ss; 56% were Le(a —), S; and 2% were Le(a —), ss. Failure to obtain correlation occurred only once in 63 corresponding samples.

In a total of 229 saliva samples from Ainu and Ainu-Japanese, 50 of group O (65%); 57 of group A_1 (62%); 28 from group B (61%) and 10 of group A_1B (71%) were secretors of A, B or H substances. The combined figures were 145 (63.3%) secretors and 84 (36.7%) non-secretors. These results compare satisfactorily with the Le^a results obtained in 338 Ainu and Ainu-Japanese, in which Le(a —) = 64.8%, and Le(a +) = 35.2%.

6. Of 100 Ainu samples tested for the P factor, 72 were regarded as P positive of which 23 samples gave good positive reactions and 49 were recorded as weak positive.

7. In Ainu, 26/27 (96%) were Duffy (Fy^a) positive by the indirect Coombs test. In Ainu-Japanese 24/24 (100%) were Duffy positive. From the results it can be predicted that the Japanese will prove to be approximately 100% Fy(a +).

8. In Ainu, 4/27 (15%) and in Ainu-Japanese 2/24 (8%) were regarded as Kell (K) positive.

9. It has been shown that cells preserved aseptically in glucose-citrate solution at 5°C. for up to 20 months give reliable results in tests for Duffy, Kell and Lewis antigens. This conflicts with opinions expressed by others that some of these antigens cannot be detected beyond a day or two after collection.

10. PTC (phenyl-thiocarbamide) taste reactions were carried out on 328 Ainu and 175 Ainu-Japanese. In Ainu, 70 (21.3%) were recorded as tasters, 237 (72.3%) as weak tasters and 21 (6.4%) as non-tasters. In Ainu-Japanese the figures were 34 (19.4%) tasters, 132 (75.4%) weak tasters, and 9 (5.1%) non-tasters. In view of the known difficulties in obtaining a reliable interpretation of taste reactions, the results are presented with some reserve.

11. Comparisons have been made between gene frequencies of Ainu and Japanese. A blending of these races is suggested by the similarity in A-B-O groups, Rh types and A-B-H salivary secretion. If such is the case the original *m* frequency for Japanese was probably greater than .60 as in Chinese and Siamese, and the *m* frequency in Ainu was less than .30 as in Australian aborigines, Papuans and New Caledonians.

12. An attempt has been made to equate genetically a component suggested by others as common to Ainu, Australian aborigines and American Indians. The factors particularly discussed were group B, the S subdivision of the M-N types, Rh_0, Rh_2, rh, rh′, rh″ and Duffy. It is considered that the genetic evidence is against a postulated proto-Caucasian component common to all three peoples. The presence of genes *r* and *r″* in Ainu and *r′* in Australian aborigines, all three of which are found in Caucasians, may be regarded as evidence that Ainu and Australian aborigines each possess a proto-Caucasian component, but not necessarily the same one. The suggested proto-Caucasian component in

Australian aborigines and in some people of India may be the same, if the common possession of r' is significant.

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SCIENTIFIC STUDY OF PRIMATE EVOLUTION.— Some students claim, or rather assume implicitly, that the phyletic relations of a series of specimens can be clearly defined from an assessment of morphological similarities even when the fossil evidence is both slight and non-continuous geologically. Others, who in the light of modern genetical knowledge are surely on firmer ground, point out that several genes or several gene patterns may have identical phenotypic effects, and that when we deal with limited, or relatively limited, fossil material, correspondence in single morphological features, or in groups of characters, does not necessarily imply genetic identity and phyletic relationship. Where, as in the study of Primate evolution, only a relatively small number of fossils is available, both with respect to the time-scale involved and to the degree of morphological diversity that exists between the fossils and extant Primates, it could be maintained legitimately that morphological resemblances allow only the broadest phylogenetic inferences. It could also be argued that since hominoid evolution does not always appear to have been divergent, a given Primate fossil could as readily be referred to some point in a network, or web, of inter-related evolutionary forms as to one of a series of diverging lines of descent. There are more than enough reasons, both here and in the tenuous nature of the biological assumptions which sometimes underlie other conclusions of physical anthropologists, for part of the controversy which characterizes the scientific study of Primate evolution. It could hardly be otherwise when what are firm statements of fact to some students are regarded as hesitant or profitless speculations by others.— S. Zuckerman. *An* ape or *the* ape? J. Roy. Anthrop. Inst., vol. 81, pts. I and II, 1951, pp. 57–68.

A STUDY OF THE LEWIS, KELL, LUTHERAN AND P BLOOD GROUP SYSTEMS AND THE ABH SECRETION IN WEST AFRICAN NEGROES

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Interest in the secretion of the ABH antigens in the saliva has been increased by the demonstration of the close association between this property and the Lewis blood group system (Grubb, '48). At present knowledge of the percentage of secretors and non-secretors and of the Lewis blood group distribution in non-European populations is limited. Schiff ('40) found 38.8% of non-secretors of ABH in a sample of 178 American Negroes in New York, which is the highest frequency of non-secretors known in any population; apparently no figures have yet been published for indigenous Africans. Miller, Rosenfeld and Vogel ('51) determined the Lewis blood groups of 200 New York Negroes and found that the frequency of the Le(a + b −) phenotype was 23%, which is similar to the frequency reported from Western Europe. In view of the association between the Le(a + b −) phenotype and non-secretor status this finding is at variance with the high per-

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centage of non-secretors observed in the Negro population by Schiff. The discrepancy would be reconciled, however, if as Miller et al. suggested some of the people of the Le(a — b —) phenotype, of which there were 16%, were also non-secretors.

In this investigation blood samples from 141 West African Negroes have been tested for the ABO and Lewis groups, and the saliva of 125 of these individuals has been tested for the ABH, Le^a and Le^b antigens. One hundred and fourteen of the blood samples were also tested for P, Kell and Lutheran groups.

MATERIALS AND METHODS

One hundred and fourteen blood samples were collected by venepuncture in Lagos, Nigeria from unmixed, unrelated, healthy, Africans; 27 blood samples were also collected by finger prick, for immediate testing, from West Africans in London. The tribal distribution is shown in table 1. The majority of the subjects were Nigerians and of these about 75% were Yoruba.

About 4 cm^3 of whole blood was placed in a sterile bottle and dispatched to London by air in iced thermos flasks. The samples arrived within 24 hours of collection. Samples of saliva from individuals in Lagos were boiled for 15 minutes within one hour of collection and transferred to sterile tubes which were sent to London by air and on arrival stored at — 20°C. The ABO, Rh and MNS groups of the 114 Lagos blood samples have been reported elsewhere (Chalmers, Ikin and Mourant, '53).

RESULTS

Lewis blood group system

The results of testing the blood samples with anti-Le^a and anti-Le^b are shown in table 2. Most of the group B and AB bloods could only be tested with anti-Le^a since no suitable anti-Le^b serum was available.

TABLE 1

Tribal distribution of 141 West African Negroes

COUNTRY	TRIBE	NUMBER
Nigeria	Yoruba	68
	Ibo	26
	Bini	15
	Urhobo	7
	Hausa	6
	Efik	4
	Ijaw	2
	Itsekiri	2
	Ngemba	1
Gold Coast	Gã	3
	Adangbe	2
	Aharta	1
	Ashanti	1
	Fanti	1
	Ewe	1
	Kyerapong	1

TABLE 2

ABO and Lewis blood groups of 141 West African Negroes

ABO	Le (a+b−)	Le (a−b+)	Le (a−b−)	NUMBERS
O	11	40	26	77
A_1	5	3	11	19
A_2	2	3	4	9
	Le (a+)	Le (a−)		
B	2	29		31
A_1B	1	4		5
Total	21	120		141

The percentage of Le(a +) phenotype is 14.9%, and of the 86 samples of groups O and A_2, 34.9% belonged to the phenotype Le(a — b —).

Secretion of ABH antigens in the saliva

All sera which agglutinated O and A_2 red cells more strongly than those of other ABO groups were formerly known as anti-O sera. Morgan and Watkins ('48) distinguished anti-

H, which can be inhibited by the saliva of secretors of all ABO groups, from anti-O which is not inhibited by saliva from secretors.

Following the technique described by Grubb and Morgan ('49), two types of anti-H sera were used: (a) eel serum, and (b) immune rabbit anti-H serum which was kindly supplied by Professor Morgan. Most of the group O salivas were tested with both anti H-sera; the groups A, B and AB salivas were tested with eel anti-H as well as anti-A and anti-B sera. The results are shown in table 3.

TABLE 3

The distribution of secretors and non-secretors among 125 West African Negroes

ABO GROUP	NON-SECRETORS	SECRETORS
O	24	44
A_1	10	9
A_2	4	3
B	8	19
A_1B	1	3
Total	47	78

The percentage of non-secretors (37.6%) approximates very closely to the observations of Schiff in the population of American Negroes.

Test for Le^a and Le^b antigens in the saliva

Owing to the shortage of anti-Lewis sera it was impossible to titrate each sample of saliva with anti-Le^a and anti-Le^b. The results are therefore based on a single tube test after the method described by Grubb ('51). To one volume of saliva diluted one-third was added two volumes of anti-Le^a or anti-Le^b. This mixture was left at 20°C. for at least 15 minutes after which time one-half volume of a 5% suspension of appropriate red cells, group O Le(a + b −) or group O Le(a − b +) was added to the mixture. The results were read microscopically after the tubes had been left for one

hour at 20°C. In the absence of inhibition visual agglutination was usually obtained, and in most cases in which the saliva had inhibited the action of the serum, negative results were obtained with the test cells. It was possible to repeat the test only with those salivas which had given doubtful results, and those which did not fit into the general pattern of reactions. The results are presented with some hesitation

TABLE 4

ABH and Lewis antigens in the saliva of 125 West African Negroes

LEWIS PHENOTYPE OF RED CELLS	ANTIGENS PRESENT IN SALIVA			NUMBERS
	ABH	Le^a	Le^b	
Le(a + b —)	—	+	—	10
	—	+	+	6
Le(a +)	—	+	—	3
Le(a — b +)	+	+	+	34
	+	—	+	5
	—	+	+	1
	—	—	+	1
Le(a — b —)	—	—	—	16
	+	—	—	16
	—	+	—	3
	—	+	+	1
	+	+	+	1
Le(a —)	+	—	—	10
	+	+	+	7
	—	—	—	6
	+	—	+	4
	+	+	—	1

because it was not possible to examine each saliva with more than one example of anti-Le^a and anti-Le^b, nor was it possible to obtain more than one sample of saliva from each individual. The results are classified in tables 4 and 5.

From table 4 it can be seen that all the individuals with Le(a +) red cells were non-secretors of ABH. The finding of Le^b substance in the saliva of 6 of these individuals is an unusual one.

Because it is known that the action of anti-Le^b is sometimes inhibited by the presence of A_1, and the group B bloods were not all tested with anti-Le^b, in table 5 the results of secretion tests on the salivas of groups O and A_2 are given separately. There were 26 O or A_2 Le(a — b —) reactors and of these 15 were non-secretors. These results do reconcile the apparent discrepancy between the 38.8% of non-secretors found by Schiff and the 23% of Le(a +) phenotype found by Miller et al. in the Negro population. Neither Le^a nor Le^b substance was found in the saliva of 23 of these O or A_2 Le(a — b —) individuals.

TABLE 5

ABH and Lewis antigens in the saliva of 75 West African Negroes of groups O and A_2

LEWIS PHENOTYPE OF RED CELLS	ANTIGENS PRESENT IN SALIVA			NUMBERS
	AH	Le^a	Le^b	
Le(a + b —)	—	+	—	5
	—	+	+	6
Le(a — b +)	+	+	+	32
	+	—	+	4
	—	+	+	1
	—	—	+	1
Le(a — b —)	—	—	—	12
	+	—	—	11
	—	+	—	2
	—	+	+	1

The antigen P

The frequency of P-positive individuals has been shown to be higher in Negro than in White populations. Landsteiner and Levine ('29) found only 2.2% of P-negative individuals among 267 colored people. Wiener and Unger ('44) found 2.3% of P-negative reactors in a sample of 73 Negroes. Miller, Tannor and Hsu ('50) reported 98.3% P-positive individuals in a sample of 300 New York Negroes; later Miller, Rosenfeld and Vogel ('51) reported a frequency of 95% in

a sample of 200. Henningsen ('50) found only two P-negative individuals in a sample of 66 Bantus. Shapiro ('51) has reported a lower frequency of P-positive than other workers; among 500 South African Bantus he found 434 to be P-positive. Chalmers et al. ('53) found 27 out of 29 West African Negroes to be P-positive. Of the 114 blood samples sent from Lagos in the present investigation 111 were P-positive (97.4%).

Kell antigen

Two Kell-positive individuals were found in the 114 examined (1.75%). Chalmers et al. ('53) did not find any Kell-positive people among 29 West Africans. Miller, Rosenfeld and Vogel ('51) reported 3.5 Kell-positive in a sample of 200 New York Negroes.

Lutheran antigen

Of the 114 blood samples sent from Lagos, 8 (7%) gave positive reactions with anti-Lu^a serum. Chalmers et al. ('53) reported 5 Lutheran-positive individuals among 29 West Africans.

SUMMARY

1. Some data on the Lewis blood group system in West African Negroes are presented. The frequency of the Le(a +) phenotype is found to be lower than in Europeans and American Negroes. Previous work indicating a high proportion of the Le(a — b —) phenotype in Negroes is confirmed.

2. Some results of testing for the ABH and Lewis antigens in the saliva of West African Negroes are given.

3. Data on the Kell, Lutheran and P blood group systems in West African Negroes are reported.

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MORPHOGENESIS. AN ESSAY ON DEVELOPMENT. By John Tyler Bonner. Princeton University Press, Princeton. 296 pp., 90 figs. 1952. $5.00. The word morphogenesis is apt to frighten the student, and even if he perseveres, the usual texts involve much mathematics and reference to unfamiliar organisms. In this book Bonner has succeeded in presenting the subject simply and attractively, or at least as simply as the subject matter allows. Fortunately the concept of growth is not restricted to living matter. Unfortunately problems of growth and form in mammals are touched on only indirectly. "Morphogenesis" then is an introduction to the subject, and a stepping stone to the larger but older works on the subject.— S. M. Garn.

THE BLOOD GROUPS OF THE DIEGUEÑO INDIANS

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The Diegueños are a Piman-speaking group of North American Indians who live in the foot hills of Southern California, near the Mexican border. Their physical type is totally different from that of other Piman-speaking Indians, and it is believed that they represent the remains of an earlier type of inhabitant of this region. It seemed worthwhile to record the blood groups of this people.

The total number of persons with Diegueño blood now only amounts to some hundreds, and of these only a few are pure-blooded. Although all the reservations, Pala, Rincon, La Jolla, Pauma, Capitan Grande, Mesa Grande, Santa Ysabel, Inaja, and Los Coyotes were visited, it was only possible in the limited time available for this work to collect 104 samples of blood, and of these only 58 were from pure-blooded Diegueños. Twenty-four samples were from persons 6/8 Diegueño and 2/8 white American, 8 from persons 5/8 Diegueño and 3/8 white, and 13 from persons 4/8 Diegueño and 4/8 white.

In assessing the degree of blood, we had to rely on several sources of evidence: the statement of the subject at interview, the personal knowledge of the subject and his family in possession of the members of the San Diego County Health Department (Indian Section), and lastly a close scrutiny of the Indian Census Roll of 1940.

MATERIAL AND METHODS

The method of collecting material and the techniques employed were those described in a previous paper on Brazilian Indians (Pantin and Junqueira, '52). The testing sera were

supplied by the courtesy of Dr. A. E. Mourant of the Blood Group Reference Laboratory, the Lister Institute. The same actual sera used in testing Brazilian Indian bloods were used in testing the Diegueños. Each blood sample was examined for the presence of the antigens A,A_1, B, C,c,D,E, M,N,S,P, Lutheran, Kell and Duffy (Fy^a). Controls of known cells were included in each test.

For purposes of calculation, only the results recorded for the 58 pure bloods have been used. The remaining results for mixed bloods are printed in table form at the end of the paper.

ABO Groups

GROUP	NUMBER OBSERVED	FREQUENCY OBSERVED	FREQUENCY EXPECTED	NUMBER EXPECTED
O	56	0.9655	0.9657	56.01
A_1	1	0.0172	0.0171	0.99
B	1	0.0172	0.0171	0.99
A_1B	0	0.0000	0.001	0.01
Total:	58	0.9999	1.0000	58.

Gene frequencies: O : 0.9826
A_1 : 0.0087
B : 0.0087
1.0000

The "Rhesus" Groups

PHENOTYPE	COMMONEST GENOTYPE	NUMBER OBSERVED	FREQUENCY OBSERVED	FREQUENCY EXPECTED	NUMBER EXPECTED
CCDee	R_1R_1	28	0.4828	0.4650	26.97
CcDe	R_1R_2	19	0.3276	0.3491	20.25
CcDee	R_1R_o	1	0.0172	0.0344	1.99
ccDE	R_2R_2	5	0.0862	0.0662	3.84
CCDE	R_1R_z	5	0.0862	0.0847	4.91
ccDee	R_oR_o	0	0.0000	0.0006	0.04
Total:		58	1.0000	1.0000	58.00

Chromosome frequencies: CDe R_1 0.6819
cDE R_2 0.2334
cDe R_o 0.0252
CDE R_z 0.0595
1.0000

Very little anti-e was available, and few bloods could be tested for 'e,' so all anti-e results were disregarded in the calculations. The frequency given for R_o is actually the total for R_o plus r, if both are in reality present.

MNS Groups

As explained in the previous paper (Pantin and Junqueira, '52), there was some doubt as to whether the anti-N sera, of which two different examples were used in each test, were giving non-specific agglutination or contained an extra agglutinin for an unknown antigen, thus giving too many apparent N-positives. After the first 19 of the Diegueño bloods had been typed, the anti-N sera were changed for a fresh pair, and only the results of the remaining 39 tests have been used for calculation.

PHENOTYPE	NO. OBSERVED	FREQUENCY OBSERVED	FREQUENCY EXPECTED	NO. EXPECTED
MMS	17	0.4359	0.4457	17.38
MsMs	5	0.1282	0.1264	4.93
MNS	8	0.2051	0.1953	7.62
MsNs	7	0.1795	0.1732	6.76
NNS	0	0.0000	0.0000	0
NsNs	2	0.0513	0.0593	2.31
Chromosome frequencies:	MS :	0.4009		
	Ms :	0.3556		
	Ns :	0.2436		
		1.0001		

The evidence is in fact insufficient to show the NS chromosome to be completely absent. It is however rare or absent in all aboriginal American populations.

The P antigen

PHENOTYPE	NO. OBSERVED	FREQUENCY
P +	33	0.5690
P —	25	0.4310
	58	1.0000

Gene frequencies: P : 0.3435
p : 0.6565
1.0000

The Lutheran antigen

PHENOTYPE	NO. OBSERVED	FREQUENCY
Lu a +	2	0.0345
Lu a —	56	0.9655
	58	1.0000

Gene frequencies: Lu^a : 0.0174
Lu^b : 0.9826
1.0000

The Kell antigen

The Kell antigen was not observed amongst these Diegueños; all were Kell-negative.

The Duffy (Fy^a) antigen

PHENOTYPE	NO. OBSERVED	FREQUENCY
Fy^a +	52	0.8966
Fy^a —	6	0.1034
	58	1.0000

Gene frequencies: Fy^a : 0.6784
Fy^b : 0.3216
1.0000

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APPENDIX

Results of tests on mixed bloods:

1. Bloods 6/8 Diegueño and 2/8 white

	A	A_1	B	C	D	E	c	M	N	S	P	Lu	K	Duffy
1	—	—	—	+	+	—	+	+	+	—	+	—	—	+
2	—	—	—	+	+	—	—	+	—	—	—	—	—	+
3	—	—	—	+	+	—	—	+	—	—	+	—	—	—
4	—	—	—	+	+	—	—	+	—	—	+	—	—	+
5	+	—	—	+	+	—	+	+	—	+	—	—	—	+
6	—	—	—	+	+	—	+	+	+	+	+	—	—	+
7	+	—	—	+	+	—	+	+	—	—	+	—	—	+
8	—	—	—	—	+	—	+	+	+	—	+	—	—	+
9	—	—	—	+	+	—	+	+	—	+	—	—	—	+
10	—	—	—	+	+	—	+	+	—	+	—	—	—	—
11	—	—	—	—	+	—	+	+	—	—	—	—	—	+
12	+	—	—	—	+	—	+	+	—	+	—	—	—	+
13	—	—	—	+	+	—	+	+	—	+	—	—	—	+
14	—	—	—	+	+	+	+	+	+	—	—	—	—	+
15	—	—	—	+	+	—	—	+	+	—	+	—	—	+
16	—	—	—	+	+	+	+	+	—	+	+	—	—	+
17	—	—	—	+	+	+	+	+	+	—	+	—	—	+
18	+	—	—	+	+	—	—	+	—	+	—	—	—	+
19	+	—	—	+	+	—	—	+	+	+	+	—	—	+
20	+	—	—	+	+	—	—	+	+	+	—	—	—	+
21	—	—	—	+	+	—	—	+	—	—	—	—	—	+
22	+	—	—	+	+	—	—	+	+	—	—	—	—	+
23	—	—	—	+	+	+	+	+	+	+	—	—	—	+
24	—	—	—	+	+	—	—	+	+	+	—	—	—	—

2. Bloods 5/8 Diegueño and 3/8 white

I	A	A_1	B	C	D	E	c	M	N	S	P	Lu	K	Duffy
1	—	—	—	+	+	—	—	+	+	+	—	—	—	+
2	—	—	—	+	+	—	+	+	+	—	—	—	—	—
3	—	—	—	+	+	—	—	+	—	+	—	—	—	—
4	+	—	—	+	+	—	+	+	+	—	—	—	—	+
5	—	—	—	+	+	—	—	+	+	—	+	—	—	+
6	—	—	—	+	+	+	+	+	—	—	—	—	—	+
7	—	—	—	+	+	+	+	+	—	+	+	—	—	+
8	—	—	—	+	+	—	—	+	+	+	+	—	—	+

3. Bloods 4/8 Diegueño and 4/8 white

	A	A_1	B	C	D	E	c	e	M	N	S	P	Lu	K	Duffy
1	—	—	—	+	+	—	+		+	—	—	—	—	—	—
2	+	—	—	—	+	—	+		+	—	+	+	—	—	+
3	+	—	—	—	+	—	+		+	—	+	+	—	—	+
4	—	—	+	+	+	+	—	—	+	—	+	+	—	—	+
5	—	—	—	+	+	—	—		+	—	+	—	—	—	+
6	—	—	—	+	+	—	—		+	+	+	—	—	—	+
7	—	—	—	+	+	+	+		+	—	+	+	—	—	+
8	—	—	—	+	+	+	+		+	—	—	+	—	—	+
9	—	—	—	+	+	—	—		+	+	—	+	—	—	+
10	—	—	—	+	+	—	—		+	—	—	+	—	—	—
11	—	—	—	+	+	—	—		+	+	+	—	—	—	+
12	—	—	—	+	+	+	+		+	+	—	+	—	—	+
13	—	—	—	—	+	+	+	—	+	+	—	—	—	—	+

NEW JOURNAL.— Under the editorship of Luigi Gedda, there is being published in Rome the *Acta Geneticae Medicae Et Gemellologiae.* Volume 1, No. 1, January, 1952, contains the following articles:

LUIGI GEDDA Genetica, Medicina e Costituzione.

PERCY STOCKS Recent Statistics of Multiple Births in England and Wales.

DAVID C. RIFE Twins and Research.

ARNOLD GESELL The Method of Co-Twin Control in Conjunction with the Method of Cinemanalysis.

M. ALDA BENCINI Contributo clinico allo studio del mongolismo nei gemelli: presentazione di una coppia di gemelle monozigotiche.

GLADYS C. SCHWESINGER The Effect of Differential Parent-child Relations on Identical Twin Resemblance in Personality.

A. FRANCESCHETTE ET D. KLEIN Oxcéphalie chez trois paires de jumeaux univitellins, associée dans un des cas à une cutis frontis gyrata.

BERTHA M. ASCHNER, LEWIS A. HURST AND LEON ROIZIN A Genetic Study of Paget's Disease (Osteitis deformans) in Monozygotic Twin Brothers.

GUNNAR DAHLBERG Die Tendenz zu Zwillingsgeburten.

HANS GREBE Diskordanzursachen bei erbgleichen Zwillingen.

THE DETERMINATION OF BODY MEASUREMENTS, SURFACE AREA AND BODY VOLUME BY PHOTOGRAPHY

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FOUR FIGURES

Photography has always been a useful tool in the hands of the physical anthropologist, but its value for producing quantitative data has received slow recognition. This first communication on the "Shivan" [2] technique indicates a potential extension of the uses of photography in anthropometry.[3]

Sheldon ('40) gave an impetus to photogrammetry when he took measurements off photographs of subjects in certain conventional postures for his somatotype classification. A further stage was reached when Tanner and Weiner ('49) demonstrated that the Sheldon measurements taken off photographs compare well with direct measurements taken off the subjects. They compared the degree of inter- and intra-observer error which may arise with either measurement and they examined some of the innate distortion effects of photogrammetry. As a result of their findings and because of the permanent nature of photographic records, it was

[1] Surgeon Lieutenant Commander, R.N., seconded from the R.N. Medical School to Oxford University.

[2] It was from the many different postures of the Hindu god Shiva that the original idea was obtained and for this reason the system has been named "Shivan."

[3] Preliminary reports were submitted to the Medical Research Council's Growth and Form Committee in 1950, and a verbal communication was given at the Fourth International Anthropology Congress, Vienna, 1952.

felt that photographs had potential value for anthropometry in general, since it appeared likely that useful body measurements might be obtained from suitable photographs, especially if several different measurements may be obtained

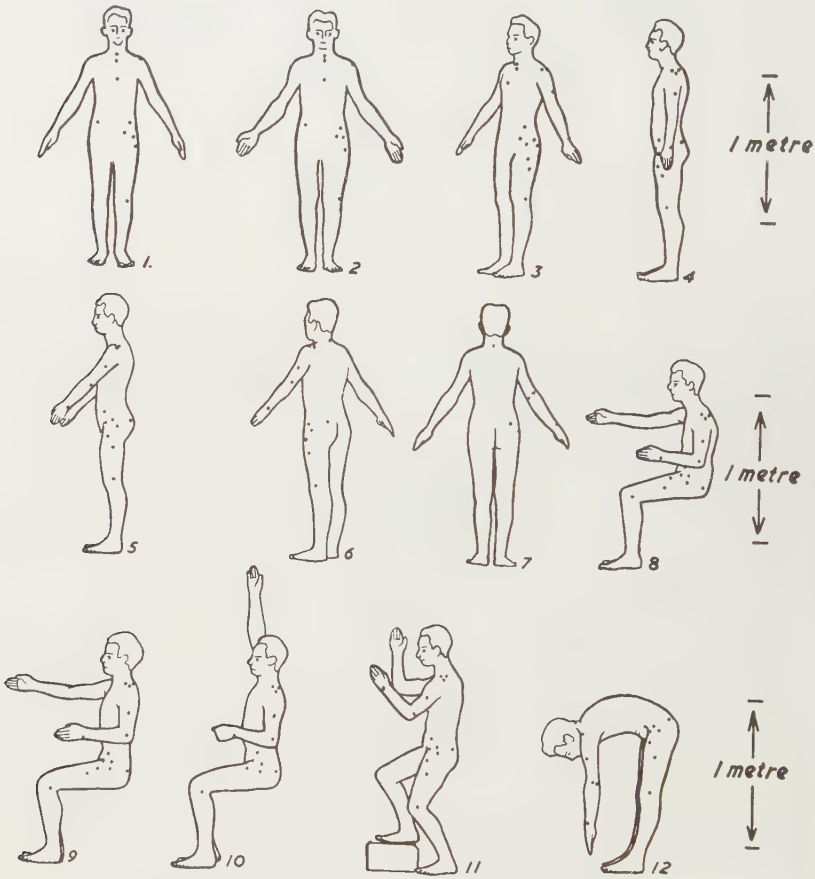

Fig. 1 Outline illustration of the (Shivan) system of postures.

from a subject in one position. With the intention of obtaining as many different body measurements as possible from a small number of photographs, a ("Shivan") system of postures was developed, outlines of which are illustrated in figure 1.

METHOD

Briefly, postures 1 to 7 are similar to the conventional somatotype postures (Dupertuis and Tanner, '50) but in general differ in that the feet are angulated outwards at 45°; the feet are placed sufficiently far apart for the legs to be vertical; and the hands, fingers and thumbs are in the long axis of the arms. Postures 1, 3, 4, 6 and 7 are all the same but the subject is rotated through 45° between each picture. For convenience, the subject is posed for the first 7 pictures on a pedestal (illustrated in fig. 2) in which the circular upper section (18 in. diameter) is on ball bearings and may be rotated smoothly upon the rectangular base. The top section has a heel rest at the back marked so that the heels

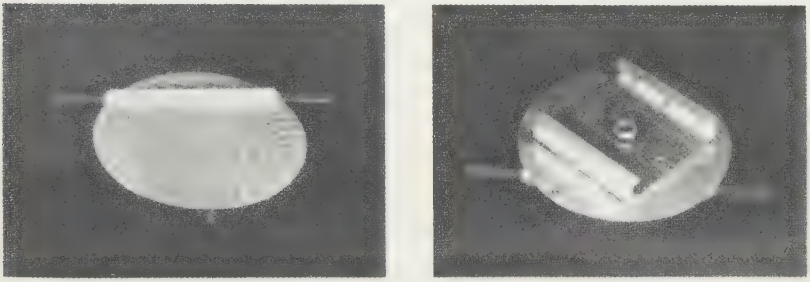

Fig. 2 Photograph of the pedestal on which the subjects stand in postures 1 to 7.

may be placed symmetrically. The outer edge is marked at 45° intervals and there is a pointer on the base. If the subjects are duly warned, they are relatively undisturbed by the gentle rotation. In posture 2 the hands are rotated through 90° outwards on the arm axis, and are returned to the initial position before posture 3. In posture 5 the arms are at 45° to the vertical and are placed forwards and parallel to one another; they are returned to their initial position again for postures 6 and 7. In the sitting postures 8, 9 and 10 the seat height is such that the thighs are horizontal with the heels comfortably on the ground and as far apart as in posture 1 and the feet pointed directly forwards. The knees are as far apart as the heels and the top of the calves should

be within one-half inch of the seat edge. In postures 8 and 9 the right arm, hand and fingers are pointed straight forwards; the left elbow is angulated at 90° with the left lower arm also pointing forwards. In posture 8 the subject sits quite comfortably and relaxed, but in posture 9 he should be rigid, drawing himself up to his full height and, keeping the shoulders square, reach forwards as far as possible. Posture 10 is also a rigid one; the left fist is clenched and the right arm held vertically. In posture 11 the right foot, pointing forwards, is placed on a 20 cm block with the left big toe just behind the right heel and the weight taken equally by both feet. Both elbows and the right knee are angulated at 90° and so arranged that they are all independently visible from the camera. Although superficially this may appear to be a difficult posture, in practice it is quite simple to pose: the subject will find that a position of comfortable balance is reached when the left knee is bent by an amount convenient to the poser. In posture 12 the knees and heels are as far apart as in position 1 but the feet point straight forwards, keeping the legs straight. The trunk is bent as far forwards as practicable on the hip with the eye-ear plane and the arms straight downwards. Common faults in posing consist of hunching the shoulders (particularly in postures 6 and 7), skewing of any part of the body, and not obtaining a 45° or 90° angulation where it is required.

Bony points and other surface landmarks which are not easily seen on photographs may be located by sticking on the skin pieces of cellotape (colored either deep blue or opaque white for photographic contrast) and cut into 1 cm squares. The precise location of the point required is made by conventionally taking some particular corner of the rectangular mark, e.g., the proximal anterior corner for acromiale. These cellotape marks have the advantage of being photographically clear; they are quickly and easily stuck on; and they allow the investigator to feel through the mark to verify its position after they have been stuck on. If two marks are

close together, confusion may be avoided by using alternative mark shapes, e.g., triangular.

From the postures as they are at present it is possible to obtain a very wide range of body measurements of both the "conventional" and "operational" type. "Conventional" refers to those used in general physical anthropology for tribal and racial studies as described by Martin ('28), Hrdlička ('20), Wood-Jones ('29), etc., and which have recently been short-listed to a profitable number by Miss Tildesley ('47). "Operational" refers to those of practical use in industry, such as the sitting eye- and elbow-height and the lengths and ranges of arm and leg movements. Besides these, surface area, radiation area (Winslow, Gagge and Herrington, '40) and body volume may be obtained from the photographs of subjects in these postures; if the body weight is known, then the body specific gravity may also be calculated by dividing the weight by the volume.

Although these postures (fig. 2) have proved useful, there is no suggestion that they are necessarily the most convenient or economical, as they may be modified in the course of further experience. For example, if the "operational" type of measurements are not required, an economy may be effected by omitting postures 8 and 11, or if the surface area or body volume is not required, then postures 3 and 6 may be left out. It may be that a few further postures might profitably be included such as a sitting back-view together with the obverse of 7–12 and 3–6; and the value of the whole series of postures might be enhanced if the rotations were at $22\frac{1}{2}°$ intervals. Again, there would probably be an advantage if a fitting rubber cap (in convenient sizes, such as that illustrated in fig. 3) is worn for head measurements. Photogrammetry of the head is being reconsidered; for the present, however, it is accepted that the height should be a direct measurement.

The photographic lay-out is illustrated in figure 4 and little further comment is required. The dotted lines are marked along the floor and permit the easier lining up of the body during the 45° rotations. A B.S.S. quality 2 meter rule is

placed at right angles to the camera on either or on both sides of the subject, and, if necessary, beneath and above the subject as well. The latter has not been found necessary. The rule acts as a convenient yard-stick from which measurements taken off the photographs may be made absolute. Illumination should be sufficient to allow an exposure of no longer than 1/25th sec. and arranged to provide good surface contour modelling. A photoflash which gives a "deadpan" appearance is not so satisfactory as correctly placed photofloods. Either a white or black screen (or

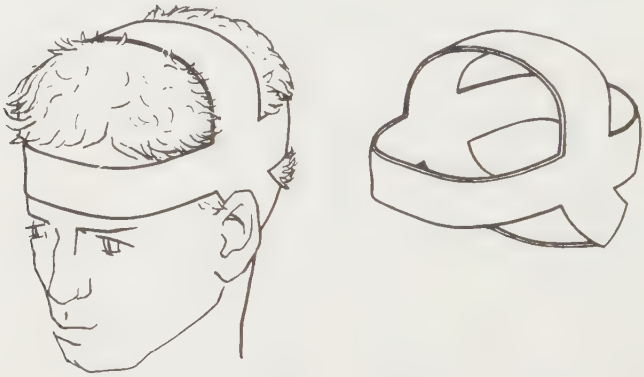

Fig. 3 Outline illustration of a skull cap to assist in the photogrammetry of the head.

none at all) should be used, the choice depending on which provides the better silhouette contrast.

Although any camera, with a suitable telescopic lens of better than 60 lines per millimeter quality will do, experience has shown that the 5 × 5 in. type camera (such as the ex-R.A.F. F.24, or its U.S.A. equivalent, the K.24) is the most convenient. A Leica camera is by no means unsuitable; in fact quite satisfactory results have been obtained with one of these at 13 m range using a Hektor 13.5 cm lens and microfile film. But the 5 × 5 in. camera with topographical base roll film (processed with some grainless developer such as microdol or promicrol) is the more convenient for a great many reasons, the most important being that (with the 50 cm

lens) the image size is such that measurements may be read directly off the negative. At the present a viewer for the 5 × 5 in. negatives is being used which gives about a 3 ×

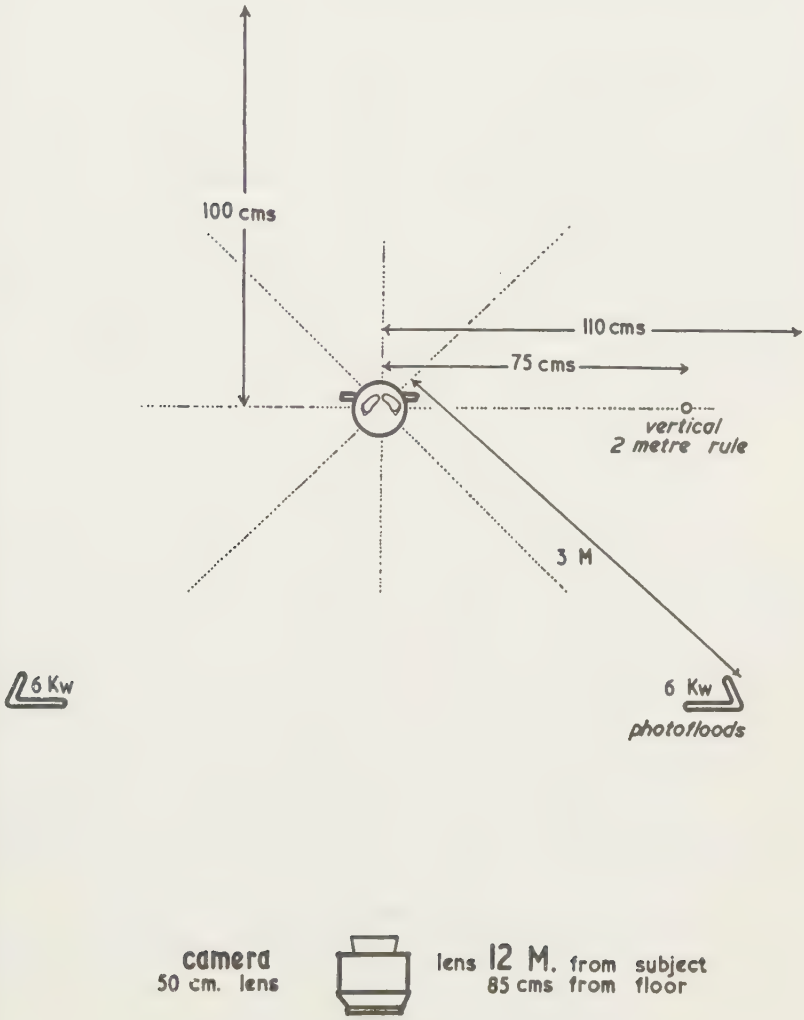

Fig. 4 Diagram of the photographic layout.

magnification: the viewer is of course an unnecessary but pleasant advantage, as readings may be obtained more quickly and efficiently and with less observer fatigue. Measurements

are taken off the negatives using a caliper of B.S.S. quality and graduated in 0.02 mm or 0.001 in. With the viewer a reading to the nearest 0.25 mm on the caliper is the equivalent of about the nearest 1.5 mm on the subject by direct measurement. For our purposes, working off the negatives has been found to be quite satisfactory.

The use of mirrors for photogrammetry has been suggested (Wenbach, '38; Schmitz, personal communication) as they offer possibilities in economy of time, negatives and filing space with a consequent reduction in posing and editorial errors, but at the same time they offer difficulties in illumination technique, cost and distortion. Schmitz has devised an ingenious means of getting around some of these difficulties; it is certainly a worthy field for future investigation.

RESULTS

Comparison of measurements by photography and direct anthropometry

A comparison of measurements obtained by the photographic method with those by direct anthropometry was carried out with the object of measuring the inter- and intra-observer discrepancies which may arise in (i) direct anthropometry, (ii) locating certain bony points and other surface landmarks, (iii) posing the subject for photography and (iv) in taking the measurements off the photographs. This analysis was accomplished by means of a balanced partially confounded design (Yates, '33; Cochran and Cox, '50; Fisher, '51) carried out on 32 different male subjects, half of whom were measured and photographed twice, the other half measured 4 times (twice each by both observers) and photographed twice. The complete block design is given in table 1. The treatments are so applied that differences directly due to any one of factors (ii) to (iv) can be estimated from duplicate measurements on the same individual, averaged over all individuals, while differences due to inter-actions between two or three of these factors can be similarly estimated from

TABLE 1

Block design for analysis of errors of marking, posing, direct measuring and photogrammetry on the subject

EFFECTS	SUBJECT'S NUMBER	DIRECT MEASUREMENT	MARKING OF SUBJECTS (X)	POSING OF SUBJECTS (Y)	INDIRECT MEASUREMENT OFF PHOTOGRAPHS (Z)	SUBJECT'S NUMBER	DIRECT MEASUREMENT	MARKING OF SUBJECTS (X)	POSING OF SUBJECTS (Y)	INDIRECT MEASUREMENT OFF PHOTOGRAPHS (Z)	EFFECTS
		By observer					By observer				
	1a	A	A	B	B	17a	A	B	A	A	
	b	B	A	A	A	b	B	A	A	B	
	2a	A	B	A	B	18a	A	A	A	A	
	b	B	B	B	A	b	B	B	A	B	
X, YZ, XYZ	3a	A	A	B	A	19a	A	B	B	A	Y, XZ, XYZ
	b	B	A	A	B	b	B	A	B	B	
	4a	A	B	B	B	20a	A	B	B	B	
	b	B	B	A	A	b	B	A	B	A	
	5a	A	B	A	A	21a	A	A	B	B	
	b	B	A	A	B	b	B	A	A	A	
	6a	A	B	B	A	22a	A	A	A	B	
Y, XZ, XYZ	b	B	A	B	B	b	B	A	B	A	
	7a	A	A	B	A	23a	A	B	B	B	X, YZ, XYZ
	b	B	B	B	B	b	B	B	A	A	
	8a	A	A	A	A	24a	A	B	B	A	
	b	B	B	A	B	b	B	B	A	B	
	9a	A	A	B	A	25a	A	B	B	A	
	b	B	B	A	B	b	B	A	A	B	
	10a	A	A	A	A	26a	A	A	A	A	
	b	B	B	B	B	b	B	B	B	B	
XY, YZ, XZ	11a	A	B	B	A	27a	A	A	B	B	XY, YZ, XZ
	b	B	A	A	B	b	B	B	A	A	
	12a	A	A	B	B	28a	A	A	B	A	
	b	B	B	A	A	b	B	B	A	B	
	13a	A	A	B	A	29a	A	A	B	B	
	b	B	B	A	A	b	B	B	A	B	
	14a	A	B	A	B	30a	A	B	B	B	
	b	B	A	B	B	b	B	A	A	B	
Z, XY, XYZ	15a	A	B	B	B	31a	A	A	A	A	Z, XY, XYZ
	b	B	A	A	B	b	B	B	B	A	
	16a	A	B	B	A	32a	A	B	A	A	
	b	B	A	A	A	b	B	A	B	A	

TABLE 2

List of measurements selected for the comparison of indirect with direct anthropometry, indicating the postures from which each measurement may be obtained

	DESCRIPTION OF EACH MEASUREMENT						NO. OF POSTURE FROM WHICH EACH MEASUREMENT MAY BE OBTAINED											
	(1)	(2)	(3)	(4)	(5)	(6)												
Longitudinal measurements																		
Height	S	M	R	T	So	Q	1	2	3	4	5	6	7					
Cervicale height			R							4	5	6	7					
Sitting height		M	R	T		Q								9				
Sitting sternale height			R	T										9				
Acromion-ulnar styloid	S												7					
Arm length		M												9				
Sternale-symphysion	S						1	2	3									
Symphysion-malleolar	S						1	2										
Olecranon-ulna styloid													8	9	10	11		
Standing crotch height			R										7					
Thigh length		M	R											9				
Leg length		M															12	
Acromion-olecranon			R											9		11		
Olecranon-dactylion			R											9		11		
Antero-posterior measurements																		
Neck AP					So					4	5							
Thorax AP outside				T	So					4								
Waist AP					So					4	5							
Symphysion AP					So					4	5							
Thorax AP	S					Q			3			6						
Transverse measurements																		
Interdeltoidale		M	R				1	2					7					
Bi-iliac				T			1	2										

Chest circ.	M	R	T		1	3	4		6	
Waist circ.	M	R	T	Q		3	4		6	7
(Crotch) Thigh circ.		R		Q	1	3	4		6	
Calf circ.	M		T	Q	1	3	4		6	7
Upper arm circ.			T	Q	1	3		5	6	

(1) Schreider ('50).
(2) Morant and Gilson ('45).
(3) Randall ('49).
(4) Tildesley ('47).
(5) Sheldon ('40).
(6) Seligman ('51).

List of skin marks required for the measurements listed above

LANDMARK (SURFACE OR BONY POINT)	POINT OF REFERENCE ON CELLOTAPE MARK	LANDMARK (SURFACE OR BONY POINT)	POINT OF REFERENCE ON CELLOTAPE MARK
4th. Costo-sternal junction	Center, lower edge.	Symphysion on thigh L	Lower edge.
Sternale	Center, lower edge.	Lower border thyroid cartilage	Center, upper edge.
Acromiale (both)	Proximal (upper medial) corner.	Mid-thigh point L	Lower edge.
Ulna styloid L	Center, proximal edge.	Mid-acromiale-olecranon length L	Lower edge.
Olecranon L	Center, distal edge.	Shoulder center (front, back, side)	Lower corners.
Crotch level on thigh L	Lower edge.	Hip center (front, back, side)	Lower corners.
Cervicale	Center, lower edge.	Lat. epicondyle humerus L	Center, lower edge.
Trochanterion (both)	Center, upper edge.	Lat. epicondyle femur L	Lower corner.
Ant. sup. iliac spine (both)	Lowest point.		

a proportion of the individuals. There was no possibility of either observer learning of the other's measurements on any individual, and in the case of the subjects who were re-measured by both observers, the average time interval between re-measurement by the same observer was three days, and his previous data were not available to him.

For this investigation 30 body measurements were selected from the literature with the intention of covering the 4 types of measurement (longitudinal, antero-posterior, transverse and circumferential). All of the measurements selected are frequently used in conventional anthropometry; a third of these are among those recommended for inter-racial comparison by Miss Tildesley ('47, '52) and two-thirds are of "operational" interest. A list of these measurements is given in table 2. Twenty-one of these measurements are of the kind which on the body are taken between certain bony points or other surface landmarks; as some of these do not show up well enough for photogrammetric purposes, 18 conventional and 6 other landmarks (listed in table 2) were marked on the subjects with cellotape spots by the method previously described. For the purposes of this communication, the results obtained on the first 10 measurements (which include examples of all the 4 types of measurement) have been analyzed and are given in table 3. This shows, for each measurement, the inter-observer errors from photogrammetry arising from marking the subjects, posing them and taking the measurements off the negatives; the inter-observer errors in direct anthropometry; the relationship of the residual variances; and the means and standard errors of the actual measurements.

From the table, 4 points deserve further mention:

1. On applying "Student's" t test to inter-observer differences on the direct measurements, significant differences were found in all but two (the olecranon-ulnare and biacromiale) of the 8 direct measurements. From the analysis of variance of the 11 indirect measurements there were some slight inter-observer differences in the marking of the subjects (in only

TABLE 3

Results of analysis of indirect and direct anthropometry. (nsd = No significant difference. NK = not known; waist and chest transverse were not taken in direct anthropometry)

	INTER-OBSERVER ERRORS				F		INDIRECT				DIRECT		
	MARKING THE SUBJECTS (X)	POSING THE SUBJECTS FOR PHOTOGRAPHY (Y)	TAKING MEASUREMENTS OFF THE PHOTOGRAPHS (Z)	DIRECT ANTHROPOMETRY	RESIDUAL VARIANCE DIRECT / INDIRECT	SIGNIFICANCE OF F	MEAN IN CM	STANDARD ERROR IN CM	OBSERVER B MEAN IN CM	DIFFERENCE BETWEEN DIRECT AND INDIRECT MEANS OBSERVER B	OBSERVER A MEAN IN CM	DIFFERENCE BETWEEN DIRECT AND INDIRECT MEANS OBSERVER A	POOLED STANDARD ERRORS OBSERVERS A AND B IN CM
Waist trans.	nsd	nsd	nsd	NK			27.10	0.030					
Chest trans.	nsd	nsd	nsd	NK			33.28	0.099					
Chest AP.	nsd	nsd	nsd	1%	0.41	0.1%	24.03	0.091	24.25	nsd	23.88	nsd	0.067
Waist AP.	nsd	nsd	nsd	0.1%	1.40	nsd	20.41	0.067	20.64	5%	19.30	0.1%	0.092
Acromiale-olecranon	5%	1%	nsd	5%	2.00	5%	37.07	0.058	36.15	0.1%	35.76	0.1%	0.095
Olecranon-dactylion	nsd	nsd	nsd	0.1%	1.30	nsd	48.07	0.066	47.69	1%	47.04	0.1%	0.087
Thigh length	nsd	1%	nsd	0.1%	1.60	nsd	59.78	0.048	59.66	nsd	58.99	0.1%	0.070
Biacromiale	nsd	nsd	nsd	nsd	2.15	1%	38.03	0.107	39.10	0.1%	39.10	0.1%	0.128
Olecranon-ulnare	nsd	nsd	nsd	nsd	0.59	5%	28.71	0.095	28.61	nsd	28.61	nsd	0.060
Waist circ. 1 [1]	nsd	nsd	nsd	1%	2.17	1%	75.01	0.103	76.20	0.1%	75.49	5%	0.174
Waist circ. 2 [2]	nsd	nsd	nsd		3.02	0.1%	75.21	0.087					

[1] Estimated by the simple ellipse formula.
[2] Estimated by Cauchy's integral.

one instance, the acromiale-olecranon) and in posing the subjects (in two instances, those required for the acromiale-olecranon and thigh length) but there was no inter-observer difference in taking any of the measurements off photographs.

2. The standard errors of the direct measurements are larger than those of the indirect measurements in the ratio of 0.1 to 0.08. In fact there are only two measurements (the chest AP and the olecranon-ulnare) in which the reverse is the case, and then by only a small margin.

3. After taking out the inter-observer differences from the direct measurements and the small posing and marking inter-observer difference from the indirect measurements, there is an average of half again as much residual variance in the direct as in the indirect type of measurement. By applying the variance ratio test this difference was found to be significant in the majority of cases.

4. The mean difference between observer A's direct and his indirect measurements is -0.18 cm and this is not significant by the standards of "Student's" t test; in the case of observer B this is $+0.24$ cm, nor is this significant; the pooled observers' direct measurements differ by $+0.06$ cm (also not significant). But the mean difference of the direct measurement between the two observers is 0.43 cm and these *are* significantly different. There is only one chance in 50 that differences as great as those observed could have occurred as a result of random deviation (in the absence of any observer bias).

There is a close relation between each direct measurement and the corresponding measurement taken from photographs. There is also confirmation of the reliability with which the photographic measurements may be obtained (Tanner and Weiner, '49). Of the measurements considered the direct measurements are on the whole less reproducible than the photographic ones. It would be premature to suggest the "superiority" of indirect measurements over the well-established direct measurements, for there are instances where each has its own advantage. An extended investigation in-

corporating many more dimensions may reveal that photogrammetry could to a large extent supersede direct anthropometry, but this possibility must await such an investigation. It seems clear that for many unconventional or operational measurements, photographs (because they make available a wide variety of postures) provides the most convenient means of obtaining the data.

Surface area and body volumes

Not only both classical and operational measurements, but also surface areas (SA), total body volumes, and the volume of parts of the body may be obtained from photographs of subjects in the Shivan postures. Surface area is a valuable unit of measurement as it is known that many physiological responses to environment are related to this factor. Roussy, in 1907, attempted to obtain the SA of a mannequin from photographs and compared his result with that obtained by a direct method, but he employed a technique in which the body is represented by a series of 56 cubes taken at certain fixed arbitrary levels. Owing to the varied shapes of human beings, no hard and fast rules can be accepted: it is wiser to consider each subject separately and individually. Using postures 3, 4, 5, 6 and 7 the body is split up into a series of levels which are selected at convenient positions so that between them there is as regularly graded an alteration in the body shape as practicable, and so that between these levels they may be considered approximately as slices from right cones. Using Cauchy's integral (Cauchy, '08) it is possible to estimate the perimeter at each level and from the slant heights between each level an estimate of the SA of the right cone slice may be obtained. From the sum of these the SA of the whole body is produced. By using vertical heights instead of slant heights the volume contained between each level may be calculated. Again, from the sum of these the total body volume is calculated, or from a sum of those of any part of the body the volume of that part of the body is deduced. The top of the head is considered as half an ellipsoid. The hands

and feet are considered separately, the former divided into a series of cylinders and rectangles, and the latter into trapezoids. Because there are no hard and fast rules for the way in which the body is divided, it is easier to calculate the SA's of the subjects with convenient shapes and also, where it is required, there is an allowance for dealing with those odd parts and oddly shaped individuals in whom a greater degree of precision is necessary. Usually, with normally shaped mesomorphs, it is convenient to divide the body into about 16 levels.

It is possible to increase the accuracy with which the SA's may be obtained from the Shivan postures in three ways. First, by increasing the number of levels into which the body is divided. This is limited by the precision with which the slant heights may be measured and would therefore vary with each observer. It would appear likely that double the number which would ordinarily be sufficient is probably the practicable limit. Secondly, if the number of angles through which the body is rotated were increased so that pictures were taken of posture 1 at say 22½° intervals, instead of 45° as they are at present, a considerable increase in the accuracy of the SA estimate would be achieved. Thirdly, it would be convenient if a line were marked all the way down the side of the body and the front and back of the body treated as separate parts. But all of these three, particularly the first two, would tend to make the method more cumbersome. An economy would be effected by increasing the rotation angles to 60° intervals. It would be unwise to increase them further (as Roussy and Wenbach do), for instance to 90° intervals, for horizontal sections of the body are very seldom perfect ellipsoids, and there is no other convenient shape to assume when attempting to estimate the perimeters. In view of the fact that the body appears to tend towards a rectangular shape, not only are 45° intervals the minimum for convenience, but also on a calculation at 90° intervals there would be a too frequent and too gross underestimate of the perimeters. For the present anyway, using the 45° rotation pictures,

an agreeable compromise has been achieved between the incompatibles of time, convenience and absolute accuracy.

The two ways of obtaining surface area which are at our disposal are the "direct" and the "formulae" methods. The direct methods may be classified into 5 main groups which are given in the following list.

Direct methods of obtaining surface area

	METHOD	DESCRIPTION
1.	Coating	Gött and Schmidt ('12) Du Bois and Du Bois ('14) Boyd and Scammon ('27) Boyd, Scammon and Lawrance ('30)
2.	Surface integration	Bartalini ('33) Bradfield ('27) Trambusti ('34)
3.	Triangulation	Lassablière ('24)
4.	Graphic	Letulle and Pompilian ('06)
5.	Linear	Du Bois and Du Bois ('15) Stevenson ('30)

The formulae methods are those in which the SA is the product of a function of one or two simple body measurements; of these formulae three deserve special consideration. Wenbach's ('39) formula gives the SA by multiplying twice the perimeter of the right thigh by the height in centimeters. Du Bois' formula (Du Bois and Du Bois, '16) which is the best known and most frequently used, gives the $SA = 71.84\ H^{0.725}\ W^{0.425}$. The Boyd ('35) formula is almost certainly the best and gives $SA = 3.207\ W^{0.7285 - 0.0188 \log W}\ H^{0.3}$. She has also suggested the use of another formula, independent of height, which is $SA = 4.688\ W^{0.8168 - 0.0154 \log W}$, and this is also very useful. Both the Boyd and Du Bois formulae give high readings for short fat subjects and the reverse for tall thin subjects (Boyd, '35).

The SA obtained by the Shivan method has the advantages of speed and ease over the direct methods and of accuracy over the formulae. The SA's of subjects 9 to 12 (from meas-

urements obtained by different observers, cf. table 1) have been calculated by the Shivan and formulae methods and are presented for comparison in table 4 and their pooled means compared in table 5. These 4 subjects were all moderate mesomorphs (3-4-3) of normal stature and so the

TABLE 4

Surface areas of subjects 9 to 12 inclusive (cf. table 1) using formulae and photogrammetry. Formulae: Wenbach 1 SA = twice mid-thigh circumference × H; Wenbach 2 SA = twice thigh circumference at crotch level × H; Du Bois SA = $71.84\ H^{0.725}W^{0.425}$*; Boyd 1 SA =* $3.207^{0.7285-0.0188\ \log W}\ H^{0.3}$*; Boyd 2 SA =* $4.688\ W^{0.8168-0.0154\ \log W}$*. (W = weight in kg; H = height in cm). The body weights used in Boyd 2 SA calculation were obtained by only one observer, so the results are pooled. Units are in square meters.*

SUBJECT'S NUMBER	BY WENBACH 1	BY WENBACH 2	BY DU BOIS	BY BOYD 1	BY BOYD 2	DIRECT MEASUREMENT	MARKING OF SUBJECTS (X)	POSING OF SUBJECTS (Y)	INDIRECT MEASUREMENT OFF PHOTOGRAPHS (Z)	SA BY PHOTOGRAMMETRY	BODY SHAPE
	SA FROM DIRECT MEASUREMENTS					BY OBSERVER					
9a	1.68	1.96	1.80	1.78	1.79	A	A	B	A	1.79	mesomorph
b	1.76	1.83	1.80	1.79		B	B	A	B	1.78	
10a	2.06	2.18	1.98	1.96	1.96	A	A	A	A	2.02	tall, fattish
b	2.14	2.27	1.99	1.97		B	B	B	B	1.98	mesomorph
11a	1.75	1.93	1.79	1.78	1.78	A	B	B	A	1.79	mesomorph
b	1.83	1.99	1.79	1.78		B	A	A	B	1.75	
12a	1.81	2.16	1.90	1.86	1.84	A	A	B	B	1.84	tall, thinnish
b	1.93	2.08	1.91	1.86		B	B	A	A	1.82	mesomorph

formulae for their SA are likely to provide a fairly accurate figure. It is clear from these tables that there is no significant difference between observers in the Shivan, Wenbach 2, Boyd and Du Bois formulae, but there is significant inter-observer error in the case of Wenbach's formula 1; and secondly the results obtained by Wenbach 2 differ sig-

nificantly from the results obtained by the other methods. The standard errors are all of the order of 0.01 m^2.

The total and partial body volumes obtained by the Shivan method are given in table 6 together with the body specific gravities.

There is no significant inter-observer difference in the results obtained on the volumes. The reproducibility of the Shivan method will be fully tested in due course by completing an analysis of the various potential errors on the 32 subject-repeats as described previously. It is hoped that a survey may be carried out in the near future on 500 or more

TABLE 5

Pooled means of surface areas of subjects 9 to 12 inclusive (cf. table 1) comparing results obtained by formulae with those of photogrammetry

METHOD	OBSERVER B	INTER-OBSERVER ERROR	OBSERVER A	POOLED OBSERVERS	DIFFERENCE BETWEEN METHODS
Photogrammetry	1.838	nsd	1.852	1.845	—
Wenbach 1	1.913	5%	1.826	1.869	nsd
Wenbach 2	2.044	nsd	2.057	2.050	5%
Du Bois	1.872	nsd	1.866	1.869	nsd
Boyd 1	1.845	nsd	1.850	1.848	nsd
Boyd 2	1.842	—	1.842	1.842	nsd

subjects using the Shivan technique. As it will be quite practicable to obtain SA on each of them by the method described above, it may be possible to establish a formula based only on bodily measurements and independent of body weight, by a multiple regression of photographic measurements against SA. Clearly there is no particular reason why varying formulae (i.e., with increasing numbers of measurements) might not be offered to provide SA to any required degree of accuracy, short of repeating the Shivan method for SA itself.

It is also possible to obtain total radiation area of the body from this Shivan method, but since this is a larger problem (Bohenkamp and Ernst, '31; Guibert and Taylor, '52), it will be considered in a separate publication.

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TABLE 6

Results of partial and total body volumes (in liters), and body specific gravity on subjects 9 to 12 inclusive (cf. table 1).

There is a significant inter-observer error in "marking" and "posing" for arm volumes, but these are of insufficient magnitude to produce any inter-observer error in measuring the photographs for the arm volumes calculations. In no other instance is there any inter-observer error.

SUBJECT'S NUMBER	MARKING OF SUBJECTS (X)	POSING OF SUBJECTS (Y)	INDIRECT MEASUREMENTS OFF PHOTOGRAPHS (Z)	VOL. OF TOP OF HEAD	VOL. LOWER HEAD AND NECK	VOL. BODY AND LEGS	VOL. ARMS	VOL. HANDS	VOL. ANKLES AND FEET	TOTAL BODY VOLUME	MEAN BODY SG.
	OBSERVER										
9a	A	B	A	1.43	2.76	56.40	4.22	0.65	2.04	67.50	0.983
b	B	A	B	1.55	2.67	58.38	4.45	0.68	1.95	69.67	0.953
10a	A	A	A	2.11	3.04	67.16	5.92	0.61	2.32	81.17	0.945
b	B	B	B	2.19	2.53	65.07	6.19	0.54	2.03	78.55	0.976
11a	B	B	A	1.95	1.88	56.50	4.50	0.65	2.33	67.81	0.975
b	A	A	B	1.55	2.19	57.38	4.04	0.61	1.99	67.78	0.976
12a	A	B	B	1.84	2.91	61.77	3.98	0.59	1.65	72.74	0.955
b	B	A	A	1.87	2.66	59.71	4.42	0.51	2.01	71.19	0.976
S.E. of the mean				2.9%	3.2%	0.75%	1.9%	2.3%	3.5%	0.65%	0.69%

have given a great deal of practical advice on photographic matters.

SUMMARY

A system has been developed by which a wide range of body measurements may be obtained from photographs of subjects in certain postures. An investigation was carried out to estimate the discrepancies that may arise from inter- and intra-observer errors of (i) direct anthropometry, (ii) skin marking, (iii) posing the subjects for photography and (iv) taking the analagous measurements off the photographs. An analysis of 10 measurements along these lines is given. It reveals that, so far as these measurements are concerned, indirect (photogrammetric) anthropometry is a satisfactory means of obtaining the data.

Surface area, total and partial body volumes may also be obtained from measurements taken off the photographs. If the body weight is known, the body specific gravity may be calculated by dividing this by the total body volume.

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DR. HOWE AND THE FORSYTH INFIRMARY. By Rollo Walter Brown. Harvard University Press, Cambridge. vii + 182 pp. 1952. $3.50. This slim book is a biography of a man and an institution. Percy R. Howe was one of the really original thinkers, whose various contributions range from the silver-reduction method of preventing dental caries, to the establishment of a department of physical anthropology at the Forsyth. The Forsyth in turn is known both as the institution where Dr. Howe worked and taught, and as the model for similar institutions throughout the world. In preparing this biography, Rollo Walter Brown has made full use of Dr. Howe's letters, published papers and the anecdotal reminiscences of his colleagues and friends. Though written in non-technical language, this volume accurately describes Percy Howe's natural bent for investigative research, and his abiding belief that dental diseases are rooted in nutritional and metabolic deficiencies. Fortunately there is a 15 page bibliography covering the period 1903–1949.— S. M. Garn.

Sickle-Cell Trait in Southern India.— The present-day inhabitants of Africa possess distinctive features in their blood — the sickle-cell trait, a very high incidence of a particular combination of Rh antigens known as R_0 (cDe), and another blood-group antigen provisionally referred to as He. So far as we know, the sickle-cell trait and sickle-cell anaemia have not been reported in people who were not either Africans or members of groups which must be expected to have an admixture of African blood. . . . The sickle-cell trait has not been found in races which do not also show a raised incidence of the gene combination R_0 (cDe).

It seemed possible that an investigation of the blood of certain Southern Indian communities might serve to refute or support the idea of a racial link between Africa and India. . . . The sickle-cell trait incidence among 191 unrelated Badagas was 8.4%, among 60 Todas 3.3%, and among 80 unrelated Irulas 30%. No sickle-cell trait was found among 443 unrelated members of other communities of the region. The incidence of the Rhesus chromosome R_0 (cDe) was at the low level found in Europeans and Northern Indians, rather than at that found in Africans. Among 60 Badagas, two individuals were of the phenotype R_0 or ccDee; among 60 Todas, two; and among 80 Irulas, none. None of the [sic] 120 blood samples contained the He antigen.

These findings lend support to the idea of an Indian migration to Africa in prehistoric times. The reverse possibility — an influx of African blood bringing the sickle-cell trait to the hills of Southern India — should have resulted in a raised incidence of the gene combination R_0 (cDe).— H. Lehmann and Marie Cutbush. Sickle-cell trait in Southern India. British Medical Journal, i, 404–405, February 23, 1952.

CORRELATIONS OF BROTHERS IN FACTOR SCORES [1]

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ONE FIGURE

It does not take much looking at identical twins to appreciate that heredity operates forcefully on general aspects of physique just as it does on blood types or other single-gene traits. Yet characters which exhibit continuous variation are extremely difficult to use in genetic studies, though by no means impossible as Mather ('49) has shown. In the first place, they lack the discrete categories necessary for direct mendelian analysis, a difference which foredoomed the efforts to mendelize the cephalic index in man. Secondly, it is not likely that the traits which have usually suggested themselves for quantitative measurement (stature, girths, head diameters) are a sufficiently direct representation — in contrast, let us say, to the A antigen and its associated gene — of the heritable entities involved. For many purposes of biometrical genetics, when it comes to be applied to man, it is probable that the obvious measurements of physique will serve better if they can somehow be transformed into

[1] Originally read at the 21st Annual Meeting of the American Association of Physical Anthropologists, March 21, 1952.

[2] This study was supported by the Research Committee of the Graduate School, from special funds voted by the Wisconsin State Legislature. The computing of factor scores, correlations and data for the analysis of variance was done on the IBM equipment of the Numerical Analysis Laboratory of the University under the resourceful guidance of Mr. Fred Gruenberger. I am greatly obliged to A. B. Chapman, J. F. Crow, C. W. Harris, T. C. McCormick and J. M. Tanner, each of whom gave me much-needed help and critical advice in generous quantities.

new kinds of measurements more directly related to heredity and its agents.

With this in mind, the author turned to factor analysis as possibly furnishing such a transformation. This consists simply of translating ordinary measurements into new terms provided by the analysis, obtaining new measurements which may be at the same time more general and meaningful anatomically and more specific genetically. These "measurements" or factors are first identified, and then the individuals are measured on them by means of multiple regression formulae. In this study, certain results obtained with these factors measurements are compared with results obtained by typical anthropometric measurements.

METHODS AND MATERIAL

In a previous study (Howells, '51) an analysis was made of 20 typical measurements of the head and body, and it was found that all the correlation, or correlated variation, of these could be explained by 7 common factors, which were tentatively identified as follows:

V_2 general body (trunk) size
V_5 long bone length
V_9 head or cranial size
V_{10} brain size
V_{14} lateral facial-cranial growth
V_{17} face length
V_{20} ear size

From the data obtained in this study regression equations have been derived (see appendix) by which an individual's measurements on each of these factors can be computed, from his known original measurements. These equations appear in table 1. (The individual factor scores, or factor measurements, are not reproduced herewith.) Thus all the information contained in the original measurements which was related to their common variation has been boiled down into 7 new measurements and partitioned more specifically.

The subjects used are 152 students of the University of Wisconsin, material which has been used in other studies

TABLE 1

Equations for obtaining factor measurements from direct measurements

	1 STATURE	2 SITTING HEIGHT	3 UPPER ARM LENGTH	4 LOWER ARM LENGTH	5 LOWER LEG LENGTH	6 BIACROMIAL BREADTH	7 BI-ILIAC BREADTH	8 HEAD CIRCUM-FERENCE	9 HEAD LENGTH	10 HEAD BREADTH
V_2 general (trunk) size	+ .086	+ .920	— .011	— .013	— .021	+ .010	— .003	— .005	— .004	— .002
V_5 long bone length	+ .344	— .095	+ .118	+ .187	+ .395	+ .012	+ .031	— .095	+ .151	— .043
V_9 head size	— .021	— .001	— .001	+ .011	+ .037	+ .002	— .014	+ .108	+ .896	— .021
V_{10} brain size	+ .374	— .311	— .030	— .051	— .299	— .033	+ .060	+ .355	— .640	+ .253
V_{14} lateral cranial growth	— .311	+ .319	+ .054	+ .025	+ .186	+ .050	+ .008	+ .043	— .048	— .010
V_{17} face length	— .029	— .117	+ .013	— .006	+ .067	+ .008	— .001	— .038	+ .001	— .019
V_{20} ear size	— .193	— .008	— .003	+ .152	+ .027	+ .032	— .018	+ .016	— .079	— .094

	11 HEAD HEIGHT	12 MINIMUM FRONTAL	13 BIZYGO-MATIC BREADTH	14 BIGONIAL BREADTH	15 FACE HEIGHT	16 UPPER FACE HEIGHT	17 NOSE HEIGHT	18 NOSE BREADTH	19 EAR LENGTH	20 EAR BREADTH
V_2 general (trunk) size	+ .005	+ .023	+ .008	+ .008	+ .010	+ .006	— .012	+ .002	+ .003	.000
V_5 long bone length	— .046	— .014	+ .045	+ .020	+ .012	— .038	+ .033	+ .009	.000	+ .004
V_9 head size	+ .004	+ .009	— .023	— .001	+ .004	+ .004	.000	+ .009	— .006	— .003
V_{10} brain size	+ .261	.000	— .202	— .150	— .094	+ .011	— .139	— .054	— .072	— .152
V_{14} lateral cranial growth	— .173	+ .041	+ .533	+ .170	+ .084	— .032	+ .131	+ .045	+ .080	+ .132
V_{17} face length	— .047	— .022	+ .094	+ .030	+ .152	+ .641	+ .231	+ .011	— .035	— .022
V_{20} ear size	— .007	+ .022	+ .021	+ .093	+ .066	+ .095	— .076	+ .017	+ .412	+ .445

(Howells, '48, '49, '51), comprising 76 non-overlapping pairs of brothers. This further comparison of brothers is, as I have implied, the ulterior reason for the application of factor analysis. The data resulting from the study consist of the following correlations:

Intercorrelations of all 20 measurements (not cited here; given as table 4 in Howells, '51).

Intercorrelations of all 7 factors (table 2, from table 8 in Howells, '51).

Correlations of pairs of brothers in 20 measurements (table 3).

Correlations of pairs of brothers in 7 factors (table 4).

TABLE 2

Intercorrelations of 7 factors[1]

	V_2	V_5	V_9	V_{10}	V_{14}	V_{17}
V_2 general (trunk) size	...	.443	.210	—.255	.515	.104
V_5 long bone length	.443	...	.371	—.505	.409	.273
V_9 head size	.210	.371	...	—.450	.255	.189
V_{10} brain size	—.255	—.505	—.450	...	—.603	—.466
V_{14} lateral cranial growth	.515	.409	.255	—.603	...	.354
V_{17} face length	.104	.273	.189	—.446	.354	...
V_{20} ear size	.126	.170	.008	—.428	.424	.127

[1] From table 8, Howells, '51.

RESULTS

In an earlier paper (Howells, '48) I furnished correlations of essentially the same set of brothers in the same 20 measurements, and later (Howells, '49) tried other methods of attempting to get some light on the comparative familial behavior of these measurements. The results were not especially satisfactory. The measurements showed marked differences in the degree of correlation between brothers, with such traits as leg length or total face height giving high fraternal correlations, and such traits as ear diameters and certain others giving low ones, most being intermediate. The outcome disproved the assumption that fraternal correlation is much the same in all traits, but was not particularly in-

formative beyond this, and indicated that we are still far from measuring the significant quantities we should be discovering.

Much the same result appears in table 3, the similar correlations of the 76 pairs of brothers used here. When we turn to table 4, with the correlations between brothers, not in ordinary measurements but in factor measurements, something much more definite appears. The contrast between the two sets of correlations is better seen graphically, in figure 1. The fraternal correlations for the measurements, on the left hand side, are scattered all up and down, as before, without other obvious significance. But the correlations for factor measurements, on the right, cluster very definitely, even though they number only 7. Five of them form one cluster having its midpoint at about .39 while the other two, long bone length and face length, are much higher, being close to .63 as a midpoint.

This is a striking result. Before considering its significance, a few other points should be mentioned.

1. Multiple correlations (such as the factor measurements are) tend to be somewhat higher than bivariate correlations of the same traits, but neither this effect nor an averaging effect seems to be responsible for the factor correlations seen here. (Nor is it clear why the first of these effects should operate on fraternal correlations.) It is true, for example, that V_{20}, ear size, has a correlation which is close to but slightly higher than the measurement correlations for ear length and ear breadth; and that V_{17}, face length, is roughly in an average position for the correlations in the measurements face height, nose height and upper face height. However, both V_9, cranial or head size, and V_{10}, brain size, are well below anything like an average figure for the fraternal correlations in the pertinent measurements (see Howells, '51, table 6): head breadth, minimum frontal, head height, head circumference and head length. (It is true that V_9 is largely determined by head length, in table 1, but such a consideration does not affect V_{10}, or change the general picture.) They

TABLE 3

Correlations of brothers, 76 pairs [1]

		PRODUCT MOMENT [1]	INTRACLASS [2]
		r	*r*
1.	Stature	.588	.572
2.	Sitting height	.350	.344
3.	Upper arm length	.475	.472
4.	Lower arm length	.607	.603
5.	Lower leg length	.635	.631
6.	Biacromial breadth	.326	.331
7.	Bi-iliac breadth	.418	.420
8.	Head circumference	.458	.460
9.	Head length	.413	.409
10.	Head breadth	.564	.556
11.	Head height	.480	.478
12.	Minimum frontal	.553	.546
13.	Bizygomatic breadth	.441	.431
14.	Bigonial breadth	.319	.322
15.	Face height	.657	.660
16.	Upper face height	.541	.543
17.	Nose height	.560	.559
18.	Nose breadth	.183	.185
19.	Ear length	.320	.306
20.	Ear breadth	.295	.283

[1] These correlations were computed from the measurements taken in standard form (deviations from the mean expressed in standard deviation units). The figures may be compared with those on a somewhat different set of pairs in Howells, '48, table 4. Errors have been discovered in the computation of the latter, so that certain of them should read: sitting height, .393; upper arm, .455; bizygomatic, .294; nose breadth, .250; ear length, .271.

[2] The product moment correlations were calculated between older and younger brothers as classes. It is more proper to assume that these classes are actually not different, that both members of a pair come from the same class without specification as to order, and to use the intraclass correlation (see Fisher, '41, or Peters and Van Voorhis, '40, p. 201). This may be computed by entering each pair twice in the correlation table (using both the *x* and *y* value of each member), or as follows:

$$r = \frac{V_b - V_w}{V_b + (n-1)V_w}$$

where V_b is the between-group variance (see table 5) and V_w the within-group variance, and *n* the number in each group, here 2. In other words, the product moment correlation is calculated as if there were a possible difference between older and younger brothers, an assumption made in previous papers (Howells, '48), while the intraclass correlation is calculated as if no such difference exists, the assumption made here.

seem, in other words, to tend strongly and independently toward a general figure in the neighborhood of .39.

2. The phenomenon of two groups — two "types" of correlations — has nothing to do with the correlations of the features or factors involved, as might be supposed at a careless glance: e.g. the fact that the fraternal correlations for long bone length and face length are both high is not a result of the mutual correlation of these traits. The correlations between factors are given in table 2. This shows that in fact V_5, long bone length, is more highly correlated with V_9, head size (.371), and with V_{14}, lateral facial-cranial growth (.409) than it is with V_{17}, face length (.273).

TABLE 4

Correlations of brothers in factor measurements, 76 pairs

	PRODUCT MOMENT [1]	INTRACLASS [1]
	r	*r*
V_2 general (trunk) size	.365	.359
V_5 long bone length	.651	.641
V_9 head size	.421	.420
V_{10} brain size	.386	.391
V_{14} lateral cranial growth	.414	.416
V_{17} face length	.617	.618
V_{20} ear size	.361	.359

[1] See footnote 2 to table 3.

3. It should be realized that the fraternal correlations in the ordinary measurements involve *all* the variance in those measurements, while those in the factor measurements involve only the common factor variance. Some of the measurements, such as nose breadth, biacromial diameter, bigonial diameter, bi-iliac diameter, the ear diameters and minimum frontal (see table 6 and appendix), have a high degree of specific variation, over half the total, which is not involved in the correlations with other measurements. Thus, for present purposes, the common factor correlations between brothers, table 4, represent a sort of simplification or purification of certain biological quantities involved, or at least a separation of cer-

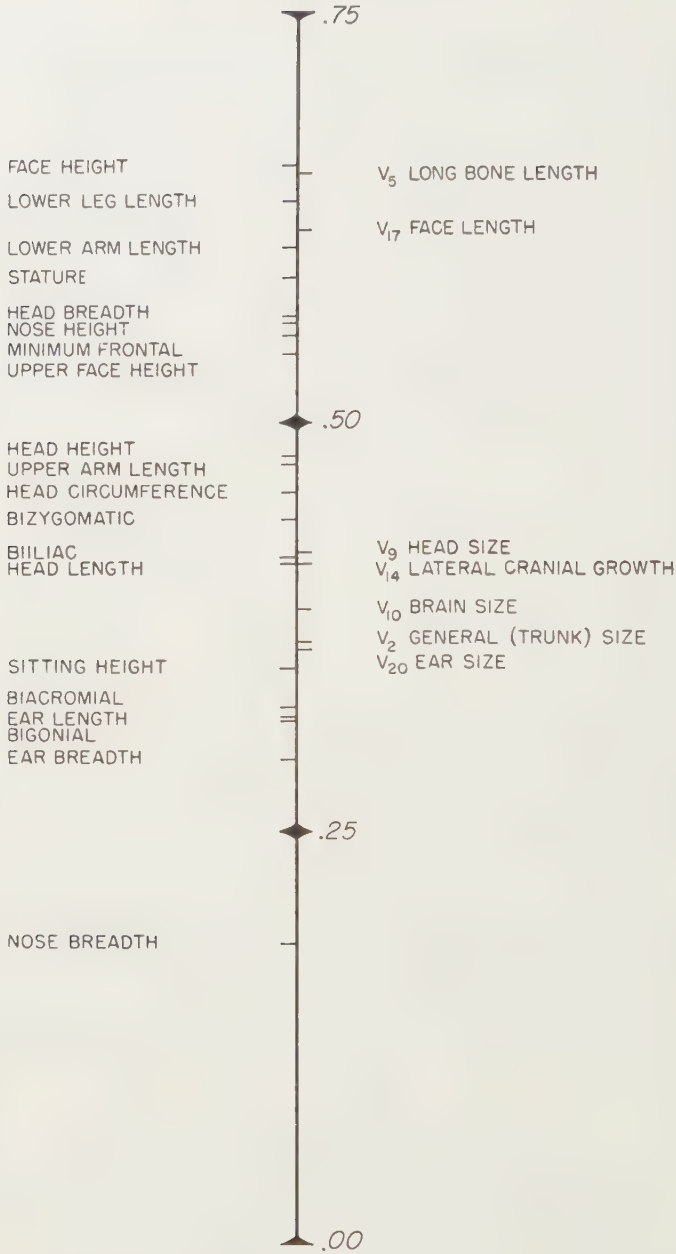

Fig. 1 Graph showing fraternal correlations in measurements (left) and factors (right). From tables 3 and 4.

tain general traits of development from whatever might be special to, let us say, the length of the humerus taken by itself.

DISCUSSION

When the brothers are measured on the factors here dealt with, which are for the moment assumed to represent mutually distinct aspects of physique, it is found that the correlation between brothers is much the same in all aspects, with two exceptions. Something is operating to make brothers appreciably more alike in the factors of long bone length and facial length than in other factors.

This may be shown in another, but very similar, way by analyzing the variance of measurements and factor measurements, as in table 5. These estimates have an identity with intraclass fraternal correlations (see Hogben, '33, p. 106), but are a useful way of looking at the same results. Of the total variance of the series in any factor, it may be seen that about 63% is contributed by variance *between* families in long bone and face length, but about 39% in the case of all other factors.

Each part of the variance — intrafamilial and interfamilial — may be affected by two kinds of cause: genetic and environmental. In these traits, we might expect the *within-family* variance to be due partly to different inheritance as between brothers (there being a one-half chance of their receiving the same chromosome from any parent in any chromosome pair), and due partly to different external influences on two brothers. The *between-family* variance is due partly to the fact that the genetic diversity between individuals of different families would be expected to be greater than within families, and partly to the differences between family environments (diet habits, medical usages, etc.). Paralleling the correlations, the ratiio of between- to within-family variance is distinctly more for limb and facial length than for other factors; however, the data do not allow any estimate of the relative importance of genetic or environmental causes in either

TABLE 5

Analysis of variance

	SUMS OF SQUARES		TOTAL	MEAN SQUARES		RATIO F [1]	PROPORTIC OF VARIAN	
	Between fams.	Within fams.		V_b (df = 75)	V_w (df = 76)		Be-tween %	W i 2
V_2	99.50	47.59	147.09	1.327	.626	2.12	36	6
V_5	114.92	25.47	140.39	1.532	.335	4.57	64	3
V_9	103.01	42.68	145.69	1.374	.562	2.44	42	5
V_{10}	70.70	31.41	102.11	.943	.413	2.28	39	6
V_{14}	76.66	31.96	108.62	1.022	.421	2.43	42	5
V_{17}	118.13	28.30	146.43	1.575	.372	4.23	62	3
V_{20}	63.23	30.28	93.51	.843	.398	2.12	36	6
Stature	119.06	32.92	152.01	1.588	.433	3.67	57	4
Sitting ht.	101.64	50.24	151.88	1.355	.661	2.05	34	6
Upper arm l.	111.39	40.53	151.93	1.485	.533	2.77	47	5
Lower arm l.	121.53	30.54	152.07	1.621	.402	4.03	60	4
Lower leg l.	123.76	28.35	152.11	1.650	.373	4.42	63	3
Biacromial	100.65	51.33	151.98	1.342	.675	1.99	33	6
Bi-iliac	107.49	44.52	152.02	1.433	.586	2.45	42	5
Head circum.	110.51	41.42	151.93	1.473	.545	2.70	46	5
Head length	106.72	45.32	152.04	1.423	.596	2.39	41	5
Head breadth	118.14	34.15	152.28	1.575	.449	3.51	56	4
Head height	112.01	40.11	151.12	1.493	.528	2.83	48	5
Min. frontal	117.21	34.87	152.08	1.563	.459	3.41	55	4
Bizygomatic	108.43	43.65	152.08	1.446	.574	2.52	43	5
Bigonial	100.17	52.11	152.29	1.336	.686	1.95	32	6
Face height	125.91	26.11	152.03	1.679	.344	4.88	66	3
Upper face ht.	117.03	35.14	152.16	1.560	.462	3.38	54	4
Nose height	118.04	33.85	151.89	1.574	.445	3.53	56	4
Nose breadth	89.46	62.35	151.81	1.193	.820	1.45	18	8
Ear length	98.78	53.21	151.99	1.317	.700	1.88	31	6
Ear breadth	96.98	54.96	151.94	1.293	.723	1.79	28	7

[1] For P = .05, F is approximately 1.46; for P = .01, it is approximately 1.77; for P = .
it is approximately 2.20.

[2] The estimate of the component of variance existing between families is $\sigma_b^2 = \frac{V_b - V_w}{n}$
being the mean square between and V_w the mean square within groups, and n the numbe
each group (2). Therefore the estimate of the proportion of this part is $\frac{\sigma_b^2}{\sigma_b^2 + V_w}$. This is
same as the intraclass correlation, cf. tables 3 and 4 (see Snedecor, '38, p. 203). These estim
should be used with some caution; they represent the variance which supposedly would
eliminated if everyone belonged to the same family; but where the F is of doubtful signific
such partition of the variance may also be meaningless.

part of the variance, and hence of the relation of such causes to the difference under discussion. Several hypotheses to account for this difference are possible (see especially Hogben, '33), but no choice can be made among them from the evidence.

1. A simple difference in genetic structure. A fraternal correlation of .5 may be expected in an idealized polygenic, continuously varying trait (see, e.g., Penrose, '49), in which the polygenes are additive in effect, and in which there are no complicating factors (external influences, assortative mating, dominance, sex linkage). The presence of dominance (so that in any contributing polygene the heterozygote effect is not the midpoint of the two homozygotes; see Mather, '49) will lower the correlation (Fisher, '18). In the present material, it might be supposed that limb length and face length are multifactorial traits of the ideal type, and that the common environment of brothers raises the correlation beyond the theoretical .5; while the other body traits would be characterized by the presence of dominant and recessive genes.

2. A compound difference in genetic structure. It cannot be regarded as settled whether there are general factors overlapping with special factors. Factor analysis allows too much leeway to determine the matter automatically. Wright ('32), using a related kind of analysis (path coefficients), reported for rabbits and chickens a general size factor, particularly important in the limbs, as well as special head and limb factors; and in a cross between large and small rabbit strains, the greater contribution of this general factor to variance in the F_2 than in the F_1 generation led him to affirm Castle's view that most genetic variability lay in such general factors. The present material does not give signs of a kind of "generalized" factor which might particularly affect both limb length and face length; certainly not in view of the low correlation of these factors with one another (see table 2). It is possible to postulate, both for the animal and human material, special growth-modifying factors, of genetic origin, which would secondarily influence limb and face length and not the other body and head factors but, while this might

affect the variability of limb length and face length on the whole, there seems to be no reason why the assortment of such postulated genes should be directly related, or linked, with those for the basic limb and face factors, and therefore no reason why such modifiers should act to increase the fraternal correlation in these factors. This possible hypothesis therefore does not seem a fruitful one.

3. An assortative factor. Positive correlation between married couples in physical traits, especially stature, has been reported at various times (cf. Penrose, '49), being of the order of .3. It might be suggested that homogamy affects limb lengths and facial length, but has no effect on other aspects of physique covered in this analysis. This is a little difficult to credit as accounting for the sharp distinction between the two "types" of correlation among our factors. However homogamy in man has not been rigorously investigated.

4. A difference in the effect of environmental influence. From the present data it is possible to make out an argument two ways. On the face of it, a higher fraternal correlation (a smaller within-family variance) would seem to indicate a greater degree of genetic determination of the trait in question, and a smaller effect of external influences. Limb length and face length would thus be more strongly under genetic control than the other traits, as already suggested by hypotheses nos. 1 and 2, and less affected by environment during growth. This might be surprising in view of past assumptions as to the effect of diet on human growth in stature, as well as such general facts as the secular increase in stature in the last century. It would, however, correspond with Wright's findings already cited, and certain other animal evidence showing that the underfeeding of cattle had a marked effect on weight and chest circumference but only a slight effect on withers height, and thus on leg length (see Brody, '45, p. 577). Furthermore, Thieme ('50) measured Puerto Ricans of several different nutritional levels and found

definite differences which were at least as great in trunk and head measures as in limb and facial lengths.

It is likely, however, that this line of reasoning may be pursued too far, for human beings at least, and that beyond some point a high fraternal correlation, or a low intra-family variance, reflects not a correspondingly high degree of genetic determination of a trait but rather the reinforcing effect of common environment in families. Newman, Freeman and Holzinger, using a few measured physical traits in their study of twins ('37), found identicals to have extremely high correlations, all of the order of .9, while fraternals had lower values, perhaps slightly higher than those of the brothers of the present study,[3] and all being greater than .5. Now it cannot be expected that the genetic likeness of brothers or fraternal twins — or the degree of correlation between them from this cause — might vary upward toward that of identical twins as a limit. For there is a qualitative difference: identical twins are not "brothers." Ordinary full brothers can hardly have an identical or nearly identical inheritance. They are not likely to have much more than 50% greater genetic similarity than unrelated individuals unless they result from homogamous matings. If the r is relatively high, or the intra-family variance low, it means parental homogamy, and possible common environmental influences, at work, *not* continuously increased genetic determination. For the fraternal differences in chromosome combinations must set limits to the likeness of brothers and should, in fact, preserve a marked proportion of intra-familial variance stemming from genetic causes. Newman, Freeman and Holzinger used their total material to estimate roughly the proportion of the variance of the differences between fraternal twins which could be assigned to these genetic causes, and found it to be at least 75% for the physical traits. If such an estimate can be supported, then the genetically determined variance must be high

[3] The traits used (stature, sitting height, head length, head breadth) did not reveal any indicative differences in correlation from trait to trait, differing in fact less than the corresponding r's in table 3.

in both the within-family and the between-family components. And if in some traits the within-family (between brother) variance is about 61% while in limb length it is only 36%, it is difficult to see how, in looking from one to the other, either the genetic or the environmental causes of difference could have been compressed by so much — the genetic causes from the general reasons stated already, and the environmental because it could have provided little leeway for compression in any case. Instead, it would appear that something *increases* the *between*-family variation in limb length and face length.[4] (For a discussion and illustration of this general point, see Lush, '45, pp. 90–96.) As to nature or nurture, this leaves us about where we were, but it seems possible to argue the environmental case with some strength within this hypothesis. A greater population range in limb length due to genetic variability as a cause should show itself within the family as well as between families. And, more simply, in human society there should be more marked differences between the environments of families than of brothers, even among college students; and thus it is possible to suppose that this expresses itself in the higher between-family variance, and higher correlations, seen in limb and face length: that these factors are somehow more sensitive to external influences than others.

It is possible that several of the causes mentioned in the above hypotheses are involved. However, the difference of the limb and face length factors from the others is so clear-cut in this particular study as to indicate that the cause of

[4] See Hogben ('33, p. 106): ". . . the r is greater or less according as differences between different values of x *or* different values of y taken at random [unrelated subjects in the present context] are large compared with differences between corresponding values of x *and* y [here, between two brothers], whatever the value of the agency which is responsible for such differences. This means that differences of environment such as tend to increase the difference between two members of the same pair affect the correlation coefficient in the opposite sense to such differences of environment as tend to make members belonging to different pairs more different." I.e., r rises with environmental differences between families.

the difference is not too complex. The fact remains that the data themselves cannot specify this cause. It is possible to suggest that the 5 factors other than limb and face length are the more "typical" in their genetic nature, and to adduce another small piece of evidence to support this. Lee and Penrose ('46) extracted the acid-soluble red pigment from human hair, getting highly reliable quantitative results. Since they got comparable concentrations from gray and white hair, and also from the hair of albinos and other persons apparently abnormal in pigment, they concluded that they were measuring the amount of chromogen, or potential color, rather than actual color present. This has the earmarks of a clearcut "genetic" trait independent of external influence, and one which is polygenic or at least multiple-allelic, varying continuously when measured quantitatively. They were able to get a sibling correlation in this trait, though for 24 pairs only. The r was .38, which is suggestively like the figures for the main group of factorial traits reported here.

CONCLUSIONS

In the study of human variation, physical anthropology is now at a peculiar stage. The long-used methods of direct measurement and observation of morphology seem to have brought up against some limitations to their usefulness — apparently caused by the failure to nourish any theoretical background for the measurements and the method — and they have lately produced nothing new. A much higher degree of theoretical sophistication has been introduced by genetics, especially population genetics, but at the same time the broad application of genetics as a method has been shackled by the very limited number of "normal" single-gene characters — mostly blood phenomena — so far available. The whole situation has lately precipitated a good deal of discussion (see especially Birdsell, '52; also McCown, '52).

Evidence has been presented in this paper that ways may be found to make measurable morphological traits more available for advanced genetic and other studies. In this case,

ordinary measurements have been transformed into factor measurements, which behave in fraternal correlations so as to suggest that the factors identified may have more genetic validity than have direct anthropometric measurements.

At any rate, biometrical genetics as a field of human variation awaits exploration by anthropologists. It is at present an area not examined by anatomical studies, nor by single-gene genetics, and certainly not by anthropometry or body build studies in their recent forms. In spite of the difficulties involved, however, it is an area into which we cannot choose but move eventually, if we expect fully to analyze individual, group or racial differences in body form, or to deal genetically with human evolution and racial history.

SUMMARY

Correlations between brothers in 20 measurements of physique, as previously reported, showed a high degree of variation between different measurements. A factor analysis of these measurements, also previously reported, produced 7 distinct factors. In the present study, correlations of the brothers in these factors are reported, for comparison with those in measurements. The factor correlations show a definite pattern: in general body or trunk size, head size, brain size, lateral facial-cranial development, and ear size, the correlations bunch around .39; in long bone length and in face length the correlations are much higher, approximately .63.

The cause or causes responsible for this difference cannot be determined from the available data; the apparently clear-cut nature of the difference suggests an underlying difference in the genetics involved. It is possible, therefore, that factors, and factor measurements, hold greater promise for such studies as biometrical genetics than do ordinary measurements.

APPENDIX

Table 1 furnishes a set of linear multiple regression equations giving the composition of the factor "measurements" in terms of direct measurements. (All of this deals only with

common factors and common factor variance, and ignores the unique factor present in each measurement, accounting for its unique variance). The form of the equations is

$$v_{ji} = b_{j1}z_{1i} + b_{j2}z_{2i} + \ldots\ldots\ldots + b_{j20}z_{20i}$$

where v_{ji} is the factor score or measurement on the V common factor j for individual i, b_{j1} is the coefficient (as given in table 1) for V factor j for measurement 1 (i.e. stature in this case), and z_{1i} is the measurement, on measurement 1 (stature) for individual i, in standard form, i.e. deviation from the mean of stature divided by the standard deviation for stature

$$\left(z_{1i} = \frac{X_{1i} - M_1}{\sigma_1}\right).$$

These factor measurements will have a mean of zero, like the standardized measurements, but unlike them will not have a standard deviation of 1.

Equations such as those in table 1 may be written in a form in which the original unmodified raw measurements may be used, without the labor of rendering the latter into standard form (see Holzinger and Harman, '41, p. 273). However, table 1 as it stands is a better way of studying the influence of given measurements on various common factors; as equations showing the composition of factor scores in measurements, it is a converse to a factor pattern (e.g. tables 5 and 6, Howells, '51), which gives the composition of ordinary measurements in factors, e.g.

$$z_{ji} = a_{j1}g_{1i} + a_{j2}g_{2i} + \ldots\ldots\ldots\ldots + a_{jr}g_{ri} \quad (+ a_j u_{ji}),$$

the last term being the unique element, not accounted for by the common factors.

The regression equations of table 1 were derived as follows. Table 6 gives the primary axis factor pattern P, equivalent to the simple axis pattern V, table 6 in Howells, '51, but not published in that paper. It is obtained by $P = VD$, D being a diagonal matrix of the roots of the diagonal values of the matrix reciprocal to Φ, the intercorrelations of the factors (table 2 herein).

TABLE 6

Primary axis pattern, P, of 7 factors

		P_2	P_5	P_9	P_{10}	P_{14}	P_{17}	P_{20}	COMMUNALITY h^2	UNIQUENESS u^2
1	Stature	.461	.769	—.004	.245	—.065	.081	.058	.919	.081
2	Sitting ht.	.985	—.001	.000	—.002	—.001	.001	—.001	.972	.028
3	Upper arm l.	—.049	.856	.008	.214	.177	—.022	.009	.663	.337
4	Lower arm l.	.040	.901	.049	.149	—.024	—.003	.135	.785	.215
5	Lower leg l.	.000	.937	.001	.000	.000	.000	.000	.879	.121
6	Biacromial	.261	.156	.152	.153	.247	.039	.040	.299	.701
7	Bi-iliac	.028	.567	.011	.514	.391	.006	.027	.408	.592
8	Head circum.	—.001	—.076	.942	.667	.581	.031	.068	.888	.112
9	Head length	—.001	.003	.984	.002	.000	.001	.000	.968	.032
10	Head breadth	.000	.000	.476	.953	.822	.000	.000	.657	.343
11	Head height	.318	.014	.638	.750	.101	.117	.225	.525	.475
12	Min. frontal	.394	—.103	.381	.255	.360	—.203	.005	.469	.531
13	Bizygomatic	—.126	.081	.294	.593	1.124	—.029	—.119	.795	.205
14	Bigonial	.000	.000	.000	—.002	.565	.000	—.001	.320	.680
15	Face height	.250	—.006	.083	.049	—.054	.789	.120	.717	.283
16	Upper face ht.	.238	—.066	.107	.113	—.174	.995	.157	.925	.075
17	Nose height	—.001	.001	—.001	—.005	.003	.870	—.009	.760	.240
18	Nose breadth	—.004	.011	.227	—.080	.135	.014	—.026	.124	.876
19	Ear length	.149	.118	.093	.238	.039	—.001	.665	.448	.552
20	Ear breadth	—.001	.001	.000	—.003	.001	—.007	.659	.435	.565

Table 6 also gives the communalities of each measurement — h^2, the contribution of all the common factors to the total variance of that measurement (the sum of the squares of the factor loadings in the orthogonal solution)— and in addition the uniqueness, $u^2 = (1 - h^2)$. The reciprocals of these latter values $(1/u^2)$ are used to form a diagonal matrix, $(U^2)^{-1}$. The transpose of P is postmultiplied by this matrix, $P' (U^2)^{-1}$, in effect weighting the values in P according to the saturation of the measurements on the common factors.

Postmultiplying the new matrix by P gives $P' (U^2)^{-1}P$, a 7×7 matrix to which is added Φ^{-1}, the inverse of the matrix of the intercorrelations of factors, to produce L. This is inverted and postmultiplied by a matrix already obtained above, $L^{-1}P'(U^2)^{-1}$, which gives the regression equations desired.

The computation and considerations involved are discussed by Holzinger and Harman ('41, ch. XII) and by Thomson ('51, ch. XV and appendix, paragraphs 9, 10 and 13). For the form of procedure used here I am much indebted to C. W. Harris.

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STANDARD VALUES IN BLOOD. By E. C. Albritton (ed.). Prepared under the direction of the Committee on the Handbook of Biological Data. United States Air Force, Wright Air Development Center, Dayton. 199 pp., 101 tables. 1951. This is one of the first sections of the Handbook of Biological Data to reach the publication stage. It encompasses a vast amount of numerical data, mostly culled from the literature, but some of it new. The contents range from the blood groups (an 11 page section containing a guide to the Wiener and Fisher Rh terminologies) to the enzymes, lipids, and blood vitamins. The coverage is uneven with a tendency to refer to older sources, and in some cases the "normal" values are far from currently-accepted norms. Nevertheless, this is a valuable achievement, especially in its attempt to standardize the measures of variability used. Especially noteworthy is the paper-saving but cumbersome system of footnotes designating sources and contributors.— S. M. Garn.

REVIEWS

AN INTRODUCTION TO PHYSICAL ANTHROPOLOGY. By M. F. Ashley Montagu. 2nd edition, xxiv + 555 pp. Charles C. Thomas, Springfield. 1951. $8.75.

This book, published late in 1951, is nominally a revision of the first edition printed in 1945. But, in comparison to its predecessor, which aroused no great enthusiasm when belatedly reviewed in this journal, it is much larger (by 60%), more completely illustrated (by 1000%), and it contains many features beyond those expected in a book so titled. Special mention should be made of the 32 photographs and illustrations depicting various primates.

An Introduction to Physical Anthropology opens with a brief history of physical anthropology, and ends with a 70 page section on techniques, anthropometrical and serological. Genetics, evolution and race are not presented as separate subjects, so that the reader first learns about genes, then mechanisms affecting gene frequencies, and finally raciation. Human taxonomy occupies a goodly share of the book, 60 pages in all, and with taxonomy, basic problems of human classifications are discussed. Fossil man follows fossil apes, and an attempt is made to clear a path through the piles of bone fragments. Human biology, primarily actuarial data, shows that physical anthropology is more than bones alone. And the fact that physical anthropology is part of anthropology is made clear by the inclusion of information on Pleistocene archaeology and early man in America.

In dealing with fossil man, Montagu lists and describes over 40 major finds, including a major share of the less well known British specimens. As a pedagogical aid, the individual specimens or groups of specimens are ordered in terms of a morphological sequence, following Weidenreich in part, but not slavishly. Montagu accepts the Gigantopithecus teeth as human. The mandibular and dental fragments of Eoanthropus are assigned to the skulls, and the skeletal remains at Tabun and Skhul are accepted as evidence of "a fairly recent admixture between Neanderthaloids and Neanthropic types." Though none of the Australopithecines are included with fossil "man," Montagu hedges on Paranthropus Crassidens (in chapter

3) as "a form very much like that from which man himself must have originated."

On many points involving the taxonomic position of now-extinct forms, a rather contemporary stand is taken. Montagu does not make every find a separate species. Readers are warned not to deny a specimen hominid status because of some one minor trait. The breeding group concept is applied to fossil man, with a not very clear explanation of morphological variability in genetical terms. However, a real opportunity is missed to point out that the forms that appear to be "variable" are usually those where we have a number of specimens, while of course no one discusses the "variability" of a form represented by just one fragment.

In writing on race-formation, the term "ethnic group" is employed as a neutral substitute for race, and by the time the dynamics of raciation gives way to the statics of classification, two additional word-replacements are instituted, "division" and "subdivision." Apart from these word shifts, the particular taxonomy employed is quite conventional, intentionally so (Montagu explains) until a genetical classification makes its debut. Thus, while Hooton's discussion of taxonomy is dismissed as one "with which no genetically-minded physical anthropologist could possibly agree" (p. 351) the scheme Montagu employs is not in major opposition. Pre-Dravidians, Dinarics, East Baltics and Half-Hamites make their appearance, though Whole-Hamites are missing! Papuans and Melanesians fall into the Negroid division, and Amerindians are to be found in the Mongoloid division. Thus, with the exception of "Nordics," the same old groups are busy exchanging genes generally at the usual stands. Since for the most part distinct populations are involved, the schema is defensible, though I see no objection to granting these populations racial status, while they last.

In the pages on human biology, data on death rates (crude and corrected) and information on disease susceptibilities are used: it is shown how environmental influences alter the length of life and limb. Constitutional differences are described too, quite properly, and the term constitution is not used only as an uneasy synonym for body-build. Some interrelationships might have been taken one step further. For example, evidence that linear individuals require more oxygen per kilogram of body weight probably indicates only that the lean individual is largely made up of tissues with high metabolic requirements. Similarly the oft-cited evidence that winter-born children are more apt to achieve prominence does not fully correct for the unequal hazards formerly faced by summer-born infants,

which lowered their chance to become famous by killing them off at the start. In considering socio-economic differences in body size, we must consider not only calories ingested, but also calories wasted in maintaining body heat. However, a full discussion of these and other subjects and their implications would have required more than the 555 pages of this book.

Naturally, in a work of this sort, we may expect inconsistencies and errors, but there is no profit in listing more than a few. The 1947 edition of Hrdlička's "Anthropometry" is called "a standard work" on page 21, and "a suggestive rather than a practical anthropometry" on page 506. Montagu has a hard time with variability; the coefficient of variation is defined as "a measure of total variability" on page 206, and a phenomenon called the "scattering of variability" is referred to on page 163. It is a very minor objection, but I am thoroughly baffled by the need to provide a special definition of a milliliter, as "approximately" 1 cc (p. 472). And if one uses the first two formulae on page 484 to calculate cranial capacity, one obtains a 600 cc difference (in favor of the women) from the same measurements.

An Introduction to Physical Anthropology is obviously intended for student use, and it is quite suited to this purpose, being simple in style, comprehensive and well illustrated. Only occasionally do the technical requirements of the subject impede intelligibility. In its completeness it does not compete with "Mankind so Far" as a text for beginners, and it is no book for the untrained instructor to teach from. However, the advanced student will be able to use the annotated bibliographies that follow each chapter, the sections on genetics and differentiation and the 70 pages on techniques. Though one might prefer a more extensive discussion of why measurements are taken and what you do with them once you have them, the following injunction is well worth quoting. "Measurements based in genuine functional biological relationships are those most to be encouraged" (p. 441). This statement, like many in the book, will be familiar to those who have attended Wenner-Gren summer seminars in Physical Anthropology.

There is more than an indication in this book of the way that physical anthropology is moving toward a unified and modern science and clear evidence of the trials and tribulations encountered on the journey.

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UNDERSTANDING HEREDITY: AN INTRODUCTION TO GENETICS. By RICHARD B. GOLDSCHMIDT. ix + 228 pp., 49 figures. John Wiley & Sons, Inc., New York. 1952. $3.75.

This eminently readable volume, by the distinguished author of "The Material Basis of Evolution," is addressed to the non-biologist. It is a skillful survey of the fundamentals of genetics and is written for those students and laymen "who do not intend to specialize in biology." The style is deft and the argument closely reasoned. Twelve short chapters carry the reader through such important topics as "Hereditary and Non-Hereditary Traits," "Elementary Mendelism," "Linkage," "Mutation," "Sex Chromosomes and Sex-Linked Inheritance," "Multiple Factors," and a final chapter which introduces the reader to certain of the more technical facts and problems of genetics, e.g., cytogenetics, chromosomal rearrangements, sex determination, biochemical genetics, and evolution.

This volume does not, of course, deal directly with the problems and methods of human genetics — a field which has considerable relevance for physical anthropology. But although the author draws his illustrative materials from botanical and *Drosophila* genetics, he does take advantage of every opportunity to relate the principles of heredity to selected aspects of human genetics, e.g., blood group inheritance, race, sex-linked inheritance, skin color inheritance, and inbreeding, among others. It is quite possible that this little book could be useful as supplemental or assigned reading in introductory courses in physical anthropology. The author provides a set of problems to accompany each chapter, a selected bibliography of advanced works in genetics, and a well-considered glossary of genetic terms.

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GROWTH AND DEVELOPMENT OF CHILDREN. By ERNEST H. WATSON and GEORGE H. LOWREY. 260 pp., 54 figures. The Yearbook Publishers, Chicago. 1951. $5.75.

E. H. Watson and G. H. Lowrey, both at the University of Michigan, have written a 260 page text on human growth and development designed primarily for pediatricians, especially those preparing for their "boards." Within the limits of their slim volume, complete with 41 tables, and supplemented by 250 selected references, there are 11 chapters ranging from heredity and prenatal factors (12 pages)

through abnormal growth (12 pages). Between are chapters on fetal growth, "normal" measurements, behavior (Gesell and a speck of Spock), endocrinology, metabolism and nutrition, to name 6 more. Normal development is stressed throughout.

Since this book is written for pediatricians rather than for college undergraduates, we need not expect it to compete with Breckenridge and Vincent's "Child Development," and it does not. Ideas, worthy of pages, are often stuffed into a single sentence. "Negro and female infants are more mature per given weight than are white and male infants" (p. 81). Sentences like this, and one on page 157 dealing with roentgenography of the mediastinum (which is rendered in the most economical of medicalese), preclude satisfactory comprehension by the undergraduate — they won't get it. On the other hand *Growth and Development of Children* is not a competitor for Nelson's "Textbook of Pediatrics," or the other encyclopaedic volumes currently available. It seeks, and to a large extent achieves a middle ground.

How successful is this book at its chosen task? By including a resumé of prenatal influences, a section on normal endocrinology, and a chapter on measurements it serves as a rapid review, and may be quite valuable to others in the field. Certainly the section on organ development is worth perusing. With the section on behavior committed to memory, one is certainly better equipped to face the parent who has read the Gesell omnibus and Spock's pocket book to boot. But it is difficult to be economical without parsimony: growth and form are hardly mentioned, and to my mind the more theoretical aspects of growth and development have been more neglected than is either necessary or wise.

Since graphical aids to physical evaluation now play an important role in school-health programs, in mass-screenings, and even in routine pediatric practice, it is well that age-size tables (including the outmoded Baldwin-Wood) and the Wetzel "Grid" and Fels "Composite Sheet" are all illustrated and explained. However, Watson and Lowrey cannot be commended on their choice of statistical terms. "Average normal values," as used by them may include just arithmetic means, or a range, presumably the two-sigma limits. Their "average distribution" is not the familiar A.D. but is really the frequency distribution (fig. 41). Throughout, age-size graphs are called "growth charts," a sin not original with them. One graph (fig. 39), said to show the rate-of-growth, does nothing of the kind. Very often graphs correctly labeled by the original authors, have been reprinted with new and inaccurate captions. It would have been cheaper, simpler and better to retain the original legends.

Yet Watson and Lowrey have shown much care both in their selection of subjects and in the choice of references that follow each chap-

ter. In dealing with endocrinology they have not confined themselves to secondary sources, but have cited prime references of obvious importance: the same is true in the chapter on metabolism. When dealing with nutrition, theoretical aspects are reviewed, but there is no information on dietary evaluation, and no references on the subject. Since dietary evaluations, unlike endocrine assays, are suitable office procedures, the omission (while intended) is still unfortunate.

As befits a text, this book is often positive on subjects that are controversial. For example, it is more satisfied with anthropometry than we are. Behavior schedules are not qualified (but the original sources do not qualify them). The difficulty of evaluating osseous stage and applying an age-equivalent is hardly broached. In the section on endocrinology the knotty problem of deciding the site of origin of many of the steroids and the distinction between those that are biologically active and those that are merely color-producing (in chemical assays) has been bypassed to a large degree. Yet, a short textbook cannot qualify every sentence with a covey of footnotes.

Watson and Lowry have produced a volume that draws together much of the voluminous data on growth and development, and emphasizes topics of current importance. Besides being useful in the sphere for which it is intended, it can serve to introduce graduate students and others to specific topics, whereas the monographs and the paste-pot compendia are too confusing. Anthropologists and others who have not yet read D'Arcy Thompson, Brody or Bonner are free to do so.

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MEASURING NUTRITURE [1]

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INTRODUCTION

The evaluation of the morphological aspects of nutritional status (nutriture) is a practically important matter. While in the U.S. overnutriture, in the form of relative obesity, may be the most disconcerting nutritional defect, much of the rest of the world struggles with life-and-death problems of undernutrition and malnutrition. Objective criteria for the assessment of nutriture are needed for the evaluation of the present status of different populations, for the demonstration of gains made by improved economic, agricultural and dietary practices, for judging nutritional deterioration in conditions of food emergency, and for the clinician's evaluation of nutriture of a given patient. The anthropologist is concerned with evaluating the degree of under- and overnutrition, not with a diagnosis of malnutrition. Nevertheless, anthropometry has an important, though limited, contribution to make to the assessment of nutritional status. This has been clearly recognized by the Joint FAO/WHO Expert Committee on Nutrition ('51, pp. 63–64).[2]

The size, form, and composition of the adult human body depend on three groups of factors: (1) genetic influences, (2)

[1] This paper was presented, in abbreviated form, as the opening address in a panel discussion organized as a part of the 22nd Annual Meeting of the AAPA, Philadelphia, December 28, 1952. The work was supported, in part, by research grant H-10(C5) from the National Heart Institute, of the National Institutes of Health, Public Health Service, and by grants from the Williams-Waterman Fund, New York, and The Nutrition Foundation, Inc.

[2] "The physical dimensions of the body are, to a considerable degree, dependent on its nutrition. Anthropometric measurements are therefore of importance in assessing existing nutritional status and in obtaining information about past nutritional history. Measurements of bodyweight in relation to height are widely used in assessing nutritional status in relation to health, and many anthropometric measurements and indices are applied and advocated for this purpose. There are, however, no generally accepted norms for the evaluation of such measurements, nor, indeed, generally accepted standard methods of making the measurements themselves. *(footnote continued on next page)*

diet, and (3) physical activity. While the genetic factors are difficult to assess quantitatively, are only incompletely understood at the present time, and largely escape rigorous analysis in man, the effects of diet and physical activity are both marked and accessible to experimental study. A consideration of diet and activity injects into physical anthropology concern for *interpretation* — the etiology and significance — of body dimensions.

The limitations as well as the descriptive power and relevance of body measurements become readily apparent when projected against the background of the recent developments in the field of quantitative analysis of body composition, *in vivo,* which have added important new internal "dimensions" to the study of human morphology. These methods should contribute significantly to the widening of the horizon of physical anthropology of the living man, stimulate rethinking of some of the basic and vexing problems (such as "body build"), and aid in the intensification of research and in the extension of usefulness of applied physical anthropology in new directions.

There has been a quietly but steadily growing pressure in physical anthropology to think in terms of function. Krogman's outline ('51) is the outgrowth of this point of view applied to the area of dental and medical research. The demands of the armed services have served as a potent stimulus for a more "functional" orientation of physical anthropology. The evaluation of nutriture is another area with important "functional" implications. The anthropometric characterization of nutritional status, going considerably beyond the height-weight relationships, represents a large and

"It is universally held that some adjustment or classification should be made for body or constitutional type, but there is no agreement as to how individuals may be classed into type, nor as to the numerical adjustments to be applied. For example, the appropriate adjustment of standards for age, particularly during the adult period, is a debatable question and there is confusion as to the meaning and validity of 'averages,' 'norms,' 'standards,' 'desirable weights,' and 'ideal weights.' Differences in norms corresponding to differences in race and climatic environment have been suggested, but adequate data to establish these on a firm basis are either lacking or have not been analyzed systematically.

"In the opinion of the committee anthropometric measurements, including relative body-weight, would be of greater practical value in the assessment of nutritional status if properly characterized norms and agreed methods were available for general application. Other kinds of measurements, particularly of thickness of the skin folds, deserve greater attention as a criterion of relative fatness and 'calorie status'."

fruitful area of applied anthropology, parallel to the use of anthropometry in machine design, improved clothing sizing, skeletal identification, identification of the war dead and other topics of military anthropometry (cf. Daniels and Hertzberg, '52; Hertzberg and Daniels, '52; White, '52).

In metabolic research, of which the science of nutrition is a branch, the physical anthropologist works as a member of an interdisciplinary team. Some physical anthropologists, deeply impressed by the possibilities of the new avenues of research, may turn into biophysicists and biochemists — and this might not be a bad idea. But a more generally acceptable mode of operation will be a pooling of the skills provided by personnel with technical competence in the various segments of human biology, impinging on the problem of nutriture. This has been the direction in which scientific work on the "whole man" has been moving (Brozek and Keys, '44) for some time, as a counter-measure to the fragmentation of the field resulting from a fairly narrow specialization imposed by the ever-growing complexity of methods and the avalanche of scientific literature.

In the present paper the references and comment will be limited to the adult man. The problem of physical development has been studied intensively and several recent reviews of facts and concepts, though not specifically focussed on the evaluation of nutriture as such, are available (Krogman, '50; Watson and Lowry, '51; Shuttleworth, '51; Garn, '52; Tanner, '52; Stuart and Stevenson, '52; Reynolds, '53; see also Macy, '42, '46, '51). Concentration on the adult man means that some important techniques for the characterization of the physical status of the growing individual, such as the methods for a quantitative evaluation of skeletal maturation (cf. Greulich and Pyle, '50) will not be considered.

Nutritional anthropometry

It is imperative to make clear both the *positive role* of body measurements (and of the newer methods for the description of body composition in terms of tissue masses) in the evalua-

tion of nutriture and the *limitations* of nutritional anthropometry. It may be useful to start with the latter. The crucial point is that nutritional status, "nutriture," is a complex concept. Consequently, the application of *any* single datum, such as an anthropometric index, grossly simplifies and at times distorts the true picture. Dietary deficiency diseases are characterized by a long line of clinical symptoms manifested by the skin, eyes, lips, oral mucous membranes, tongue, teeth and gums, skeleton (rachitic deformities, osteomalacia), as well as the nervous, circulatory (beri-beri heart disease, edema) and endocrine systems (simple goiter in iodine deficiency) (Jolliffe et al., '50; Jolliffe, '51; for a critical analysis of the validity of some widely employed criteria of nutritional deficiencies see Darby, '47, '50). Many of the clinical signs are not specific indicators of a particular type of malnutrition. At times, they may be of non-nutritional origin altogether (beri-beri polyneuropathy vs. a similar clinical picture in severe diabetes, infectious polyneuritis, or heavy-metal poisoning; Jolliffe et al., '50, p. 54).

The clinical procedures used in an individual diagnosis of a deficiency disease, in nutritional surveys, and in experimental investigations have been supplemented by laboratory methods (Youmans and Patton, '42). These are concerned principally with the assessment of the levels of essential nutrients in bodily tissues and fluids (thiamine content of muscles sampled by muscle biopsies, concentation of ascorbic acid in leucocytes and in blood plasma, excretion of riboflavin in the urine, level of hemoglobin in the blood) and of metabolic abnormalities which develop when these nutrients are not available to the body tissues in sufficient amounts (e.g., elevation of pyruvic acid in the blood in the case of thiamine deficiency) (Goldsmith, '50; cf. also Jones, '51; and Goldsmith, '49). In fundamental laboratory studies concerned with the impact of a nutritional deficiency on the human organism the physiological and psychological functions must be also considered (cf. Keys et al., '50; Keys et al., '45; Brozek, Guetz-

kow and Keys, '46; Brozek, Guetzkow, Mickelsen and Keys, '46).

Underweight is a general clinical finding which may result from the deficiency of a variety of dietary factors (calories, protein, vitamins, and other nutrients). In starvation, the decrement of body weight may be masked, in part, by the accumulation of edema fluid. On rapid refeeding fat is laid down much more rapidly than the muscle and other (visceral) "active" tissues, so that neither weight nor the superficial appearance of the patient are a safe guide to the degree of recovery from semistarvation.

Introduction of methods for the study of body composition serves the purpose of attaining greater precision in the description of nutritional status, with special reference to calorie nutriture. However, it should be stressed forcefully that data on body dimensions and on body composition characterize only one facet of nutritional status, man's physique. Consequently, the term "anthropometric index of nutritional status" seems to be ill chosen, as it may be given — over-enthusiastically by the physical athropologists, antagonistically by the clinical nutritionists — a much more comprehensive meaning than can be possibly justified. The fact that most of the nutritional indexes suggested in the past — such as Franzen and Palmer's arm-chest-hip index, '34; Oppenheimer's arm/chest circumference nutritional quotient, '09; Pignet's coefficient of robusticity, stature — (weight + chest circumference); and numerous height-weight indexes (cf. Krogman, '41) — fail to reflect relevant and adequately defined aspects of human physique, simply adds insult to injury.

Nutritional deficiencies, such as scurvy, may be found in individuals of good, "normal" body dimensions (Sinclair, '48). Patwardhan ('52) pointed to such symptoms at Bitot's spots on the conjunctiva, associated with vitamin A deficiency; phrynoderma — the "toadskin" — also probably due to vitamin A deficiency; and angular stomatitis — superficial erosions and fissuring at the angles of the mouth — associated with riboflavin deficiency. Pellagra may develop in obese

("overnourished") individuals. On the other hand, good health is compatible with a wide range of values for heights and weights. Patwardhan ('52) stressed the fact that the child growth and the structure of the adult human body is materially influenced by genetic, as well as nutritional and other (activity) factors. However, a conclusion that anthropometric measurements are of little or no value in the assessment of nutritional status is not warranted. Obviously, the diagnosis of pellagra must be based on the lesions, especially the lesions of the skin, which constitute the pellagra syndrome. The differences observed between national and racial groups demand establishment of separate norms, plus intensive research on "ideal" rates of child growth and ideal body composition of adults, evaluated with reference to such criteria as morbidity and length of life. Barely a beginning has been made in this difficult field, but the material and administrative obstacles do not negate the validity of such an approach.

In this country, the insurance data on relative weight (at the time of the insurance application) present a gross but useful sample of the data needed. It has been well established, even though a satisfactory interpretation of the facts is not at hand, that marked "overweight" represents a serious medical hazard. Using death rates of "standard risks" as equal to 100, the mortality of moderately overweight men equals 142, for markedly overweight men 179 (Armstrong et al., '51). For women the respective values were 142 and 161. A large part of the excess number of deaths was accounted for by the degenerative diseases of the heart, the arteries, and the kidneys. The incidence of deaths due to diabetes was three times as large as would be normally expected. It is this kind of a validation which is needed for a meaningful definition of "ideal" body weight and body composition. It is conceivable that in societies widely differing in mode of life, physical environment, and genetical background different sets of "ideal" values would apply.

While it must be clearly recognized that anthropometry cannot be used for a diagnosis of deficiencies of special nu-

trients, the mass and the composition of the body do represent a fundamental criterion of nutriture. These characteristics may be evaluated on the basis of anthropometric data (including representative measurements of the principal body tissues — bones, muscles, and subcutaneous fat), measurements made from x-ray photographs, and the newer biophysical and biochemical methods for the breakdown of the gross body weight into fat and lean body mass and its cellular, mineral, and fluid components. No attempt will be made here to present a detailed exposition and the critique of these methods. This has been done in a separate review (Keys and Brozek, '53). A survey of the older literature was presented elsewhere (Brozek and Keys, '50, '51).

Let us first consider, very briefly, those criteria and methods which fall professionally into the anthropologist's tool box. These are three in number: (1) body weight and external body dimensions (cf. Škerlj, '53), (2) thickness of the subcutaneous fat estimated from skinfolds, and (3) x-ray photographs adapted for soft-tissue analysis.

What is needed as the first step in a metric evaluation of under- and overnutrition is simple means for predicting an individual's "standard weight," taking into account not only height (as is done in the current tables, descending for the most part — directly or indirectly — from the '12 medico-actuarial tables) but also the general skeletal framework. Equations for predicting the standard weight have been made repeatedly in the past but most frequently the "predictors" have included body dimensions which represent bony frame *plus* soft tissues. Thus Breitmann ('32) used chest circumference, in addition to stature and sitting height. It is obvious that for a man with a large amount of fat around his chest one would obtain a "standard" weight which would be too high, and in computing man's relative weight (actual as percentage of standard) we would *underestimate* the degree of "overweight." This error has been liberally repeated by subsequent investigators (cf. Cureton, '47, p. 141), a fact that shows a lack of clarity of thought on the basic issues, a de-

ficiency that no mass statistics or the high reliability (consistency) of the anthropometric data can remedy. In measuring chest circumference, Masler ('45) proposed to hold the tape tightly in stout individuals and more loosely in slender individuals in order to compensate for some subcutaneous fat. Should such a complex variable be used as the chest circumference, rather than a well-defined bony dimension, a correction based on the *measured* thickness of the skin plus the subcutaneous tissue is preferable to the highly subjective adjustment of tension on the measuring tape.

For young adult women Turner ('43) derived an equation for calculating "normal" weight on the basis of height, chest width, bi-iliac width, bitrochanteric width and the girth of wrist and ankle. Pryor ('40) provided tables of standard body weights for boys and girls 1 to 17 years of age, and men and women grouped in 6 age categories (18, 19–20, 21–24, 25–30, 31–40, 41 and over), taking into account the width of the chest, measured at the nipple level (unfortunately, with no pressure!) and yielding three groupings, and the bi-iliac diameter, with 9 subgroups.

The usual weight standards are descriptive rather than normative and give arithmetical means of body weight for a given height and age. While the increase in body weight (and in the fat content of the body; Brozek, '52; Brozek et al., '53) during maturity is a statistical fact, incorporated into the "standards," it is not necessarily a desirable trend. Tables published by the Metropolitan Life Insurance Co. ('42, '43) contain "ideal" weights applied to women and men 25 years old and older. These tables were constructed on the basis of median weights, at ages 25 to 29 for women and about age 30 for men (Dublin, personal communication). A range of weights was given for three sizes of the skeletal frame (small, medium, large) at each inch of height. Unfortunately, the reader is not informed of the procedure used in arriving at these particular values nor is he instructed as to how to proceed in classifying body frames when he is attempting to apply the tabular values in practice.

Skinfold-thickness measurements have been made for more than three score years (cf. Richer, 1890) but the practical application of this method has been hampered by the lack of such basic prerequisites as adequate skinfold calipers (and consequently the absence of truly useful norms) and of agreement on locations at which to measure the skinfolds. This decision is not to be arrived at by a formal process of voting by this or that official body but must be based on correlational and experimental studies of the relative validity of the different skinfolds as criteria of fatness. Data on correlations between skinfold measurements on young and middle-aged men and the fat content of the body, estimated from specific gravity, have been presented (Brozek and Keys, '51). In this study the values of the coefficients of correlation were lowered by the error of measurement inherent in the density determinations due to a use of an average rather than an individually determined correction for the air remaining in the lungs and respiratory passages during underwater weighing.

In a study on experimentally induced obesity in man (Brozek et al., '53) in which 10 men were measured at the start, middle and end of the experimental period, the skinfold measured under the chin showed a poor correlation with specific gravity ($r = 0.631$). In the ascending order, the coefficient of correlation was 0.789 for the skinfold measured at the thigh above the patella, 0.811 below the scapula ("back"), 0.834 above the nipple ("chest"), 0.835 at the back of the upper arm, 0.884 at the abdomen (next to the navel), and 0.904 above the iliac crest in the mid-axillary line.

It may be that deposition of fat during rapid laying down of fatty tissues in different parts of the body surface differs from the distribution present in slow gain in body fat as is seen in the process of aging. Relevant information has been obtained by comparing a group of young (range 23 to 29, mean 25.2 years) and middle-aged (range 53 to 57, mean 54.6 years) men (Brozek, '52). Their body fat, estimated from specific gravity, was 14.4 and 25.2%, respectively ($\triangle = 10.8$,

an increment of 75% when expressed in reference to the younger men's mean). The skinfolds also increased but the magnitude of the increase varied remarkably (6% for thigh above patella, 12% for the back of the upper arm, 15% above the iliac crest, 24% under the chin, 36% at the abdomen, 47% under the scapula, and 71% at the chest).

Sex differences are also of interest. Data on 53 skinfolds in adult men and women were examined by Edwards ('51), with the average fold of the females being more than one-and-a-half times as large as in average-weight males. Significant differences were noted in the distribution of subcutaneous fat. The age factor did not receive adequate consideration (no mean ages were given). Data are available (Brozek et al., '53) for comparing the older men, considered in the preceding paragraph, with a group of women of similar mean age (56 years) but wider age range (46–67 years). In the older women, body fat accounted for 39.8% of body weight, a value higher by 13.6% than the men's mean (25.2% of body weight). Using men's mean values as the reference, the women's skinfold showed a markedly higher value at the extremities (a difference of 76% in upper arm, 83% at the thigh above patella). In the trunk only the abdominal skinfold indicated such a trend (with a difference of 34%) while the "waist" (above iliac crest, 13.5%) chin (7.5%) and back (6.6%) differed little and the chest skinfold, which may not be exactly comparable in the two sexes, showed an apparent trend in the opposite direction (−11.3%).

It is only through this type of biological validation that the meaning and usefulness of the skinfold measurements will become clarified.

A good deal of exploration of the techniques of measuring skinfolds was done in the Laboratory of Physiological Hygiene, University of Minnesota, under the direction of Dr. A. Keys. This work has been carried out, in part, in the framework of the Committee on Nutritional Anthropometry,

Food and Nutrition Board, National Research Council.[3] Several experimental models of skinfold calipers were constructed and tested, and work is in progress on the final design of a simple but accurate instrument. The effect on skinfold thickness of the tension exerted at contact points of the calipers was systematically examined (Sandler, '52). In England recommendations for the design of skinfold calipers are being formulated by the Technical Sub-committee of the Medical Research Council (Clements, personal communication).

The measurement of the thickness of subcutaneous tissues from x-ray photographs, as well as of the breadth of muscle and of bone, introduced by Stuart et al. ('40), has been used in a number of studies on the growth of children, including investigations directly concerned with nutritional status (Stuart and Kuhlman, '42). Most measurements were made on roentgenograms of the leg, at the level of the greatest width of calf. The calf is very well suited for this method of assessment of the absolute and relative development of the three tissues but, biologically, it appears to be a questionable indicator of the general level of fat content. No data have been reported in the literature on the correlation of the calf "fat breadth" and the mass of the subcutaneous or total body fat, as has been done for the skinfolds (Brozek and Keys, '51). Unpublished data on skinfolds measured at this level in a group of women indicate a very low correlation with the fat content estimated from specific gravity but skinfold measurement at the calf is hard to make, especially in individuals with a thick *panniculus adiposus,* and the low correlation might be due to the large errors of measurement. Thus the question of validity of calf fat-breadth and its parallelism to total body fat remains unanswered. Garn and Durkatz ('53) observed that the thickness of subcutaneous tissue at the calf follows the direction of weight fluctuations but they lacked

[3] A. Keys (chairman), L. I. Dublin (morbidity and mortality statistics), Grace A. Goldsmith (clinical applications), W. M. Krogman (ratings of body build and anthropological measurements), H. C. Stuart (growth and development), J. Brozek (secretary).

estimates of the fat content of the body which would have provided a proper reference point for calculation of percentage changes. Both absolutely and relatively, other areas, especially the trochanteric region, have shown greater gains than the calf.

The values of the tissue components in the leg were reported for adults from the Fels Research Institute for the Study of Human Development (Reynolds and Asakawa, '50). The study was made on 100 men and 100 women, ranging in age from 19 to 70 years (men's mean age 37.8, women's mean 38 years). It is a pity that the relation between age and fat was examined in terms of a correlation coefficient rather than traced in the form of a trend. The age range is so large that the initial increment in fat with age, clearly reflected by all height-age-weight tables and demonstrated by the specific gravity and the skinfold technique (Brozek, '52), was probably followed by a decrement in fat. This would result in a curvilinear trend, not adequately described by a coefficient of product-moment correlation. Norms, based on the whole sample of 100 individuals (i.e. without age differentiation) are given for absolute and relative tissue breadths. The fat breadth corresponds to 9.3 vs. 17.9% of the total calf breadth in men and women, respectively; for muscle the means are 57.3 vs. 53.2%, for bone 33.7 vs. 28.8%.

The biophysical and biochemical methods for the analysis of body composition will be presented in their barest outline. They are based on determination of (1) body density, (2) elimination or absorption of gases, and (3) total body water and the special fluid "spaces."

The specific gravity of the "lean" body mass, free from "non-essential" fat, has been estimated as 1.099 (Behnke, '41, '42). While the calculations on which this value was based do not hold — e.g. the estimate of the "essential" fat component of the lean body mass was too high — the value of 1.100 appears to be a limit approached by very thin individuals and could be accepted as the specific gravity of "lean body mass," whatever may be its actual chemical composition. Ad-

dition of fat, with its low density, decreases the density of the body and one can estimate the added fat in a particular individual for whom body density has been determined. The body volume, needed for calculation of body density (mass per unit volume), is obtained most readily by weighing an individual under water. The fact that a correction of the underwater weight must be made for the amount of air remaining in the lungs and the respiratory passages complicates the technique (Brozek et al., '49). Theoretically, the determination of body volume by air displacement should be possible. In applying the principle to the living man, the temperature changes in the air chamber have represented a major obstacle to obtaining valid readings (Metz and Keys, '50). A successful modification of the technique was reported by Wedgwood and Newman ('52).

The relationship between the fat content and the density of eviscerated carcass has been examined in guinea pigs (Rathbun and Pace, '45), rats (DeCosta and Clayton, '50), pigs (Brown et al., '51), and cattle (Kraybill et al., '52). For man an equation for predicting the fat content on the basis of specific gravity (a ratio of body density to the density of water) has been developed by Rathbun and Pace ('45). Provision of normative data (Brozek and Keys, '50; Osserman et al., '50) is complicated by the presence of marked age trends.

On a more thorough examination of the matter, the densitometric estimation of fat is a more complex problem than it has appeared at first. The principal point (Keys and Brozek, '53) is that when an adult man becomes heavier, he does not add pure "fat," in the chemical sense, but a *complex* tissue the density of which is higher than that of human fat.

Behnke ('41, '42, '45) showed that, theoretically, it is possible to estimate the fat content of the body from *elimination* of the gaseous nitrogen. Nitrogen, an inert gas, is dissolved in body fluids and in body fat in the ratio of about 1 to 5 (9 cm^3 per kilogram of fluid, 52 cm^3 per kilogram of body fat). It can be removed from the tissues by placing the body

in an oxygen atmosphere, its volume determined and divided according to the solubility of nitrogen in water and fat. From the "fat" fraction of the nitrogen volume the weight of fat may be calculated.

The procedure involved a long period of observation (6 hours and more) and is not useful for routine measurements. The possibilities of estimating body fat on the basis of *absorption* of non-toxic, inert gases characterized by a high fat-water solubility ratio, taken up by the animal organism in an enclosed system, were explored by Lesser, Blumberg and Steele ('52).

In the last decade the greatest amount of developmental work has been devoted to the "tissue morphology" of body fluids. Within the framework of the studies on body composition, carried out under A. R. Behnke's direction at the Naval Medical Research Institute, Bethesda, Md., Pace and Rathbun ('45) have shown that the water content of guinea pigs differing widely in body weight is fairly constant when expressed in reference to the fat-free body weight. Similar observations had been made earlier by Ashworth and Cowgill ('38) for the rat. Pace and Rathbun made an important further step, pointing out that fat may be considered as a "diluent" of the fat-free body mass and the fat content of the body may be estimated from the known amount of total body water (% fat = 100 − % water/0.732, where 0.732 is the water fraction of the fat-free body mass). In their study the water content of the guinea-pig carcass was determined by desiccation. In man, the total body water was obtained by the use of the radioactive isotope of hydrogen, tritium (Pace et al., '47; Prentice et al., '52) and by a variety of other substances (cf. Edelman et al., '52; Hardy and Drabkin, '52; Levitt and Gaudino, '50; McCance and Widdowson, '51a). In studies on body composition, in which both specific gravity and total body water were determined (Messinger and Steele, '49; Osserman et al., '50; Kraybill et al., '51) the use of antipyrine (Steele et al., '50; Brodie et al., '51) was the method of preference. A satisfactory agreement between the two

methods of estimating the fat content was obtained, a fact which was due, in part, to an interlocking set of assumptions. This problem has been discussed critically elsewhere (Keys and Brozek, '53).

In nutritional studies several other "fluid" spaces are of interest, in addition to the total body water. Thus the extracellular fluid, measured most frequently as the thiocyanate space, has shown a marked increase in undernourished individuals. After 6 months of semistarvation the value, expressed as percentage of body weight, was 34% as compared with 23.5% in individuals maintained on an adequate diet (Henschel et al., '47). In undernourished Germans, who had just returned from Russian camps for prisoners of war, the mean value was 38.6%, and after nutritional rehabilitation 23.9% (McCance and Widdowson, '51).

The difference between the total body water and the extracellular space represents the intracellular water (cf. Berger et al., '50). From this value McCance and Widdowson ('51) have calculated the weight of the cellular tissues, assuming that cells contain 67% of water. These authors estimated the minerals as 7% of the fat-free body (cf. Widdowson et al., '51) and calculated body fat either from total body water or by subtracting from the total weight the weight of the extracellular fluid, cell mass, and the weight of the minerals in the skeleton.

When the estimation of fat from body density is combined with measurement of extracellular fluid and an estimate of bone mineral (Keys et al., '50), it is possible to obtain the cell ("active tissue") mass as body weight less these three components (fat, extracellular fluid, and bone mineral). Thus we have two different methods for the partitioning of the body into 4 compartments.

Implications for physical anthropology

Nutritional anthropometry is, in essence, an application of physical anthropology to a practical problem of evaluating an important aspect of nutritional status. But this is by no

means the whole story. First of all, the problems provide a stimulus for directing the anthropologist's research more systematically toward a quantitative assessment of soft tissues. Because of the crucial role of nutrition in health and performance capacity, the study of nutriture significantly widens the application of the techniques of descriptive anthropometry. Within the discipline of physical anthropology, the evaluation of nutriture provides an invitation to learn new techniques, such as specific gravity determinations. The introduction of the new biophysical and biochemical methods for the analysis of body composition, *in vivo,* provides the physical anthropologist with important new criteria needed for the analysis of body build. The glaring absence of some data, e.g. of quantitative information on individual differences in bony mass, should stimulate further research. However, I believe that the most important effect will be the rethinking of some of the fundamental concepts of physical anthropology of the living man, especially of the crucial concept of body build, forced by the impact of the new data and the new ideas elaborated in the framework of the study of body composition. These techniques answer, in part at least, Howells' prayer for fresh means of quantification in the study of body build (Howells, '52, p. 93).

Sheldon ('42, p. 8) has stated, without citing empirical evidence, that "endomorphs" are of low specific gravity, "mesomorphs" (and "ectomorphs!") of high specific gravity, but did not follow up this important lead. Thus he missed an opportunity for linking up his ideas with the biophysics of body composition, just then introduced by Behnke and his collaborators (Behnke, Feen and Welham, '42; Welham and Behnke, '42). The relation between body build and body composition, evaluated on the basis of specific gravity and the water content, was examined some 10 years later by Dupertuis et al. ('51a, b). The significant finding was a correlation between endomorphy ratings and the two criteria of leanness-fatness ($r = -0.853$ for specific gravity, $r = -0.797$ for the percentage of total body water). Using the prediction

equation based on specific gravity, the endomorphy ratings, ranging from 1 to 7, would correspond to 1.1, 6.6, 12.3, 18.1, 24, 30.1, and 36.3% of fat. The validity of this prediction equation is limited by the characteristics of the samples (men, age 18 to 46).

This was a valuable study, indicating the possibilities of interpreting and describing "body build" in terms of body composition. Strangely enough, this conclusion was not drawn and its far-reaching implications were not brought out. The authors have turned the logic around and placed emphasis on the prediction, from endomorphy ratings, of body fat and total body water.

Reynolds and Asakawa ('50) applied the method of tissue analysis, based on the measurements made on roentgenograms of the calf, to the study of extremes of body build, defined in terms of Sheldon "types." Using the means of normal adults as the reference point, the fat-breadth values of the extreme endomorphs, mesomorphs, and ectomorphs were 164, 82, and 82% for men; 155, 85, and 70 for women. The muscle-breadth values are 104, 109, and 90 for men; 112, 110, and 87 for women (note the high muscularity of the female endomorphs!). The bone-breadths equal to 107, 104, and 91 (with a high value for endomorphs!) in men, 100, 103, and 91% in women.

While the roentgenogrammetric technique in general and its application in this particular instance have their technical limitations, the study is an important link in the chain of developments in the study of the internal structure of the body, defined in anatomical terms, rather than of the surface appearance and "intuitively" derived components of human physique.

The studies of Dupertuis et al. ('51a, b) were not concerned with the thorny problem of permanence of the somatotype, but the authors took a definite stand on this point stating that "one of the premises of the constitutional anthropologists is that the components of an individual's somatotype remain constant, at least after skeletal growth is completed" (Dupertuis et al., '51a, p. 680). In view of the correlation, established

in the study itself, between fatness and endomorphy ratings, together with the known mobility of the fat depots on changing the level of the caloric intake and during aging, the validity of such a statement would appear questionable. When the hypothesis was subjected to a critical test, in the context of the Minnesota starvation-rehabilitation experiment (Keys et al., '50), it could not be sustained. Lasker ('47) has shown, by using both measurements made on photographs and somatoscopic ratings, that 6 months of caloric reduction were associated with a marked decrement in endomorphy, a moderate decrease in mesomorphy, and a marked increase in ectomorphy. Averaging the mean component values obtained metrically and in two independent sets of ratings, one made under Dr. J. M. Andrew's supervision in Professor Hooton's laboratory at Harvard University, we obtain a mean somatotype of 3.4-3.9-3.3 during the control period, and 1.8-2.6-5.6 at the end of semistarvation.

This does not mean that there are no "constitutional," permanent bodily characteristics. It simply means that we cannot seek them by techniques which involve soft tissues. More importantly, the biophysical and biochemical studies of body composition allow an *interpretation*, in more biological terms, of the changes portrayed by the somatotype ratings. The body weight, which decreased on the average from 69.5 kg during the control period to 53.6 kg at the end of 24 weeks of semistarvation, was broken down into bone mineral (2.8 kg; no change during starvation), extracellular fluid (17.1 and 17.2 kg), body fat (9.7 and 2.8 kg), and "active tissues," calculated by difference (39.9 and 29.2 kg). On percentage basis, at the end of starvation the body contains a good deal less fat, less muscle, but substantially more water, the excess of which was manifested, in part, as a clinical edema (Keys et al., '50, p. 284).

Evidence on changes in body build (and body composition) during maturity is provided also by the studies on aging. In a large sample of U. S. Army separatees, somatotyped under Professor Hooton's direction at Harvard University ('51),

Newman ('52) observed a steady rise in the first component of body build (endomorphy, "fat"), with mean ratings of 4.1 at age 18 and 4.8 at age 35, paralleled by a decrement in the third component (ectomorphy, "attentuation"), with mean values of 4.6 and 3.8, respectively. The second component (mesomorphy, "muscularity") showed at first an increment (3.6 at 18, 4.1 at 27) but rapidly attained a plateau, with some indications of a decrement in the next decade.

Aging is another area in which we have data on body composition, data which are incomplete as yet but which again throw light on the somatotypist's handiwork. In men who, on the average, had a standard body weight for their age and height, and averaged 20.3, 25.2, 46, 50, and 54.6 years, the mean fat percentages estimated from specific gravity were 9.9, 14.4, 22.2, 24, and 25.2 (Brozek, '52). Similar trends have been established for women (Brozek et al., '53).

These data, taken together, make unacceptable the thesis proposed by Dupertuis et al. ('51), stating that "The normal increase in body fat with advancing years, and the loss of fat through exercise and/or a restricted diet, have a direct effect on body specific gravity but should not influence the rating of the somatotype."

Of course, one should not forget that cross-sectional studies can yield only general trends. All of us know examples from among our acquaintances who do not share the average trend of increase in body weight with age. However, the absence of difference in gross body weight does not mean that body composition remains identical. We have compared (Brozek, '52) a group of younger and older men (mean ages 25.2 and 52.1 years) matched for height (177.1 vs. 176.9 cm) and weight (75.6 and 75.7 kg). The mean specific gravity of these "overweight" young men and "underweight" middle-age men was 1.0651 and 1.0528, corresponding to 16.5 and 22.6% of body fat.

In the complex of conditions referred to as environment, food is one of the very potent factors moulding man's body and mind (Keys et al., '50). Montagu ('51) noted that there

is a definite evidence for the effect of nutritional factors on body form, citing the shape of the head as an example. However, the nutritional facet of human ecology is largely an unexplored field. Montagu (ibid, p. 429) believes that a study of the relationship between food and some of the differences exhibited by the various ethnic groups of mankind is a highly promising field of research.

Coming back once more to those important studies and provocative comments by Dupertuis et al. ('51), we find the suggestion that for older subjects the difference between their actual weight and the weight at the age of 21 would give an approximate measure of added fat. Actually, this is not too bad a proposition but it oversimplifies the matter. Age changes in body weight, well documented by all the height/weight tables do not represent a simple addition of so much fatty tissue. There is, simultaneously, a decrement in the lean body mass, as the weight of the added fat increases *faster* than the gross body weight. For men 176 cm tall, the standard weight increases from 67.6 kg at the age of 20 to 76.8 kg at the age of 55 (increment of 9.2 kg). A "standard" amount of fat, calculated from a parabolic prediction equation (Brozek, '52, p. 787), increases from 10.3 to 25% (7 to 19.2 kg, an increment of 12.2 kg), while the lean body mass decreases from 60.6 to 57.6 kg (a decrement of 3 kg).

Having discussed, at some length, Sheldon's system of somatotyping and some of its intellectual descendants, let us look at another potentially promising approach to the problems of body build, the factorial analysis of the intercorrelations between body measurements. Factor analysis can do a useful job in radically reducing the number of measurements needed for an effective description of man's physique and in defining the fundamental "dimensions" of the human body. Yet I wish to emphasize what Wolfle ('40) said some 12 years ago, namely, that both the correlational analysis (by which sets of pairs of measurements are converted into a table of correlation coefficients) and the factor analysis (by which a table of intercorrelations is converted into a table of factor

loadings) are tools developed for a parsimonious description and an inductive interpretation of the relationships between the *initial measurements.* Thus the *choice* of measurements assumes a crucial role. In the face of very complex and arduous statistical gymnastics, involved in factor analytic computations, it is easy to lose out of sight this simple yet fundamental truth.

So far, not a single study known to the writer started with a comprehensive set of measurements. These should include, obviously, an adequate sampling of pure-tissue measurements and thus provide "anchors" for the location and interpretation of the principal "vectors of the body" (cf. Thurstone, '35). This means that we cannot be satisfied with conventional measurements, as has been done in the overwhelming majority of the existing studies (e.g. Cohen, '38, '41; Hammond, '42; Thurstone, '46; Burt, '47; Rees, '50).

This is also true of Howells' work ('52) which utilized measurements obtained by Dupertuis ('50) but was based on correlating pairs of *persons,* measured in reference to a set of anthropometric characteristics, rather than on correlating pairs of measurements obtained on a group of subjects.

In Howells' study the emergence of a bipolar factor, with individuals rated as extreme endomorphs having positive, the ectomorphs having high negative loadings, is especially significant. This result would be predicted from a body-composition analysis of ectomorphy, characterized by low values of fat and muscle mass. Ectomorphy was also defined not as an independent aspect of the body build but as a negative pole of both endomorphy and mesomorphy, in Sills' investigation ('50). Sills' work is notable for the inclusion of subcutaneous fat determinations in the factor-analyzed anthropometric data. The fat index (sum of the fat measurements/stature) had the highest loading on the "endomorphy" factor.

There is another interesting point in Howells' study, brought up by Lasker ('52) who considered the body-build factors in the light of anthropometric data obtained in the Minnesota Ex-

periment. Lasker noted that those measurements which were most subject to change in starvation had highly positive scores on the first bipolar (endomorphy-ectomorphy) factor, the factor which accounted for the major fraction of the variance in the study of extreme somatotypes. Although some inconsistencies were revealed by the comparative analysis of the amount of starvation decrements and the factor scores, Lasker concluded that the factor represents a measure of the nutritional status. Limiting "nutritional status" to "calorie status," such an interpretation appears proper.

At times, it is the inconsistencies in the data and the theories which finally lead to a better understanding of the phenomena studied. In Howells' study, two dimensions — the chest depth and the bi-iliac diameter — had a fairly high score on the endomorphy-ectomorphy factor but changed little or practically not at all (bi-iliac diameter) in semistarvation. These dimensions have been determined, as Lasker surmised, as *bony* dimensions, using a good deal of compression. We were hardly surprised that starvation resulted in a minimal change in these measurements. It may be more surprising, perhaps, and it is certainly more instructive, that they are included in the endomorphy-ectomorphy factor. It is obvious that this factor does not represent a purely soft-tissue over- or under-development but that the bony trunk size, of quite a different biological meaning, is incorporated in the same factor. This may be an unavoidable result of Howells' procedure in which he *starts* with extremes of body build *based* on a somatoscopic evaluation. The initial limitations of somatotyping cannot be overcome, in such circumstances, by any amount of mathematical labor or astuteness.

The repeated observations of the factor-analysts force us to conclude that ectomorphy can hardly be considered any longer as a "primary structural component," as postulated by Sheldon. This difficulty was felt by Hooton and his associates (Hooton, '51) who replaced ectomorphy ratings from photographs by a height-weight index and struggled valiantly to relabel the "component." But the attraction of a trini-

tarian system seems to have been just too overpowering to allow a radical solution of this Gordian knot. Perhaps the anatomist's scalpel, plus a balance, would be a more appropriate instrument for this operation than the traditional sword.

COMMENT AND SUGGESTIONS

Montagu has stated, as a fundamental rule of applied anthropology, that "when a problem requiring the assistance of anthropometry is presented, all those parts of the body, and only those, should be measured which are capable of throwing some light upon that problem" (Montagu, '51, p. 441). As far as the evaluation of nutritional status is concerned, the overwhelming majority of measurements made in classical anthropological investigations on the living man (including such recent additions as the meticulous study of Irishmen reported by Hooton and Dupertuis, '51) are irrelevant.

Those professionally interested in the problem of quantitative evaluation of nutriture will find little guidance in the handbooks and manuals of physical anthropology (Hrdlička, '39; Stewart, '52). Martin ('28) paid only minimal attention to such matters as the measurement of skinfolds. However, he stated clearly that the development of subcutaneous fat cannot be used as *the* index of nutritional status because the latter is a much more comprehensive concept [4] (Martin, '38, p. 205). In Montagu's most recent contribution to the textbook literature, neither the anthropometric methods for tissue analysis nor the recent biophysical and biochemical techniques have been mentioned. This sin of omission is expiated by the positive attitude toward development of measurements based on genuine functional biological criteria, and by the author's disarming humor: "The development of such biologically based measurements is to be preferred to the slavish repetition of those embalmed in anthropometric manuals, not excluding the present one" (p. 442).

[4] It involves criteria of health and fitness which are beyond the reach of anthropometry, in the accepted usage of this word.

Anthropometrically, the correct road to a quantitative analysis of human physique has been clearly outlined by a Czech anthropologist, Matiegka ('21) who published an important paper on this subject on these very pages of the American Journal of Physical Anthropology, edited by his life-long friend, Aleš Hrdlička (Škerlj and Brozek, '53). The fact that this paper has been completely overlooked constitutes one of the major calamities of American physical anthropology, having allowed an undue amount of elbow-grease and brain power to be diverted into inspectional somatotyping while the measuring anthropologists lacked a sophisticated conceptual framework combining the componental and holistic view of human body build (cf. Hunt, '52).

In his day, Matiegka was dismayed by the sterility of much of the business of body measurements. He was interested in developing a system for a quantitative description of man's physique which would make sense anatomically, biochemically, and physiologically. Impressed by the surge of applied psychology (psychotechnology, psychotecnics), he wanted to make the concept of body build practically more useful as well as theoretically more sound. In this framework he developed a method for estimating the amount of the principal body tissues — bone, fat, and muscle — tissues which exhibit considerable interindividual differences, play different and well-defined structural and functional roles, are amenable to a quantitative anatomical (post-mortem) analysis, and can be estimated with a reasonable accuracy in the living man. The weight of the skeleton was calculated from height and 4 bony diameters (width of humeral and femoral condyles, wrist and ankle). The volume of the skin and subcutaneous fat was estimated on the basis of 6 skinfolds and body surface. The muscle-mass calculations were based on the circumferences of the extremities (corrected for the thickness of the skin and subcutaneous fat) and the stature.

This pioneering venture was not without limitations. Thus, for many purposes, it will be desirable to estimate the weight of subcutaneous and of total body fat rather than of skin and

subcutaneous fat, calculated by Matiegka. One may object to Matiegka's mathematics and dispute the precise value of the coefficients included in the prediction equations. One may deplore the absence of a rigorous anatomical derivation or subsequent validation of these equations. But one cannot deny the basic soundness and fruitfulness of this approach, attempting to describe the human body in terms of the constituents of body weight.

It may be useful to cite Matiegka's anthropometric analysis of the body composition of two women, one undernourished, the other obese. They were of similar height but one weighed 39.5 and the other one 90 kg. The weight of the skeleton was estimated at 8.4 and 8.1 kg (21.3 vs. 9% of body weight), that of muscles at 12.7 and 18.8 kg (32.2 vs. 20.9%), and of the skin and subcutaneous fat at 2.3 and 47.7 kg (6.9 vs. 53%). Using the weight of the skeleton as the reference point (100%), the muscle mass corresponded to 151 and 233%, and the skin plus fat tissues to 33 and 591%, respectively. In this system, then, the "body build" is characterized in terms of the skeletal mass (which could be assigned a value indicating the individual's position in the normative group), and muscle and fat mass expressed in terms of the bony mass.

Parenthetically, it may be noted that bone was used as a reference point also by Reynolds and Asakawa ('50) in their evaluation of sex differences in fatness. The breadth of "bone" was measured on the antero-posterior roentgenograms of the leg, at the level of greatest breadth of calf, as the sum of the breadths of tibia and fibula. The breadth of "fat" represented the sum of the thickness of medial and lateral subcutaneous adipose tissue (plus skin). Expressing "fat" as percentage of "bone" brought out clearly the difference in the fatness of men and women, with mean values of 28 and 62%. This procedure is preferable to computing the relative breadth of fat on the basis of the *total* breadth of calf (which already includes the fat breadth). Surprisingly enough, Reynolds has not carried this reasoning to the logical conclusion and has not computed a muscle/bone index.

It may be noted that the correlations between fat and bone, and muscle and bone are negligible (— 0.03 and 0.08 for men, 0.01 and 0.05 for women), indicating that these characteristics vary independently from each other, while the correlations with total breadth of calf are sizable (0.55 and 0.88 for men, 0.66 and 0.79 for women).

The new biophysical and biochemical methods for the analysis of body composition provide welcome criteria for predicting, from anthropometric data, the amount of certain body constituents (especially fat from skinfolds; Brozek and Keys, '51). The quantitatively-minded anatomist (who may wear, perhaps, a physical anthropologist's hat) has important contributions to make in providing data on variables, such as the skeletal and the muscle mass which are not accessible at this time to a direct biochemical determination *in vivo*. Valuable basic data result from comprehensive chemical postmortem analyses of body composition (Mitchell et al., '45; Widdowson, McCance and Spray, '50) but there is little likelihood that this information will accumulate very rapidly.

In anthropology, the possibilities of the use of photographs for nutritional research demand further exploration, starting with questions of pose (cf. Gavan et al., '52) and ending with the validation of a system of ratings and measurements by cross-comparison with simultaneous analyses of body composition. Provision of adequate pictorial standards of reference and thorough (descriptive) checklists is an essential part of the development of this potentially important tool.

While there is little difficulty in rating a fanatic "muscle-builder" or a grossly obese individual, within the more normal range there are definite limitations to one's ability to differentiate between the fat and muscle components of the soft tissue on the basis of photographs. Some anthropologists (Škerlj) prefer to speak of hyper- and hypoplasia, referring to the amount of undifferentiated soft tissues. This may be an honest recognition of inherent limitations of all anthroposcopic and photogrammetric methods, but for nutritional pur-

poses the evaluation of muscle, fat, and bone mass remains the real goal.

While the concept and methods of body composition provide a valuable basis for the quantification of both nutriture and body build, they do not exhaust all aspects of either of these two concepts. As far as nutriture is concerned, the point has been clearly stated in the earlier section of this paper and needs not be belabored here. "Body build" may be broken down into three facets: (1) Body composition (i.e. composition of the whole organism, characterized by the mass of the principal tissues or in terms of chemically defined constituents, such as proteins and mineral salts); (2) body structure (i.e. tissue composition of body segments, especially limbs — the internal "body form"), and (3) the external body form — up to the present the anthropologist's principal concern.

It appears useful to describe body build not by any single pseudoglobal "index" but by a profile indicating, numerically and graphically, the individual's position on the several "primary somatic factors" which can be measured and the measurement of which serves a useful purpose. Such a procedure would be somewhat analogous to the development in the field of mental testing in which it was found desirable to replace, for some purposes, the concept of "general intelligence" by scores in tests of "primary mental abilities" (Thurstone and Thurstone, '41; Guetzkow and Brozek, '47). Along similar lines of thought, Škerlj's differentiation between the constitutional, plastic, sexual, and morphological aspects of body build (body "types," in his terminology) represents a nonmathematical approach to this problem, using lepto-eurysomia, masculinity-femininity, and the amount and the distribution of soft tissues as the 4 "aspects" of the body build (cf. Škerlj, Brozek and Hunt, '53).

With reference to the assessment of nutriture it becomes obvious, even on a superficial examination of the problem, that the number, precision, and complexity of anthropometric methods used in different contexts must differ substantially. The extremes are represented, on one hand, by an evaluation of

the nutritional status (as gauged from gross body weight) of a population under conditions of dietary emergency and, on the other hand, a detailed quantitative study of changes in the amount and distribution of soft tissues and the density of bones (Mack et al., '49; Keys et al., '50; Brown and Birtley, '51) in a well-controlled laboratory study. Nutritional surveys, carried out under normal conditions but with limited personnel and facilities, fall somewhere in between. The busy clinician asks for "practical" methods of evaluating the nutritional status, for methods which are rapid, accurate, and economical (Pollack, '50).

In nutritional anthropometry, as in the pediatrician's appraisal of child development, "the main obstacles for the general acceptance of more detailed anthropometric studies are the lack of generally accepted selections of measurements, lack of adequate statistical material for the evaluation of such measurements, and the complicated character of many of the suggested examinations" (Kornfeld, '47, p. 113). A satisfactory solution of these problems represents a challenge to physical anthropologists who are anxious to play their part in the contemporary world and who emphasize the integration of the sciences of man rather than the "independent status" of physical anthropology as an academic discipline.

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THE TOPOLOGY OF THE HUMAN PREMAXILLARY BONE

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THREE FIGURES

INTRODUCTION

The topology of the human premaxillary bone has been a perennial problem of anatomy, maxillo-facial surgery and physical anthropology. Two schools exist concerning the fate of this bone in man. One view holds that the maxillary bone overgrows the premaxillary bone ectofacially, so that, except for the anterior nasal spine, the definitive premaxillary bone is not present on the superficial aspect of facial skeleton (Keith, '48). The contrary view claims that the maxillary bone fuses with the premaxillary bone ectofacially at the incisive suture and does not overgrow the premaxillary bone (Inouye, '12; Chase, '42). As a result the premaxillary bone is represented in the adult in a topological position similar to its fetal location.

If the absence of the premaxillary bone on the human face is a "specific human character" (Wood Jones, '47), the resolution of these conflicting views has special significance to physical anthropologists and students of human phylogeny.

This paper is concerned with an evaluation of these views. The conclusion is reached that in man: (1) the premaxillary bone and maxillary bone fuse at the incisive suture and (2) the maxillary bone does not overgrow the premaxillary bone.

CHRONOLOGY

To analyze this problem, it is essential that observations be made on embryos from 18 to 40 mm CR length (7–9 fetal

weeks of age). The ossification centers of the premaxillary bone and maxillary bone appear in embryos of 15 to 35 mm CR length and the loss of the incisive suture occurs in embryos of less than 40 mm CR length (Augier, '31; Noback and Robertson, '51). Embryos over 40 mm CR length cannot yield critical data on the problem under consideration since the obliteration of the incisive is an accomplished fact at this age.

PREOSSEOUS MORPHOLOGY

A terminological confusion exists in some of the literature between the term osseous process and the term process when applied to the embryonic connective tissue masses in the branchial region.

The bilateral maxillary processes are dorsal projections of the first branchial arch. By growing anteriorly and fusing with the globular portions of the median nasal processes they supply the anlage of the upper jaw and together with the inferiorly situated mandibular processes they will form the external oral aperture. All of the approximative growth and fusion of these embryonic processes occurs before the appearance of the membrane bones in this region. The relative contributions of the maxillary process and the median nasal process are an accomplished datum before osseous differentiation commences. The area of extent of the premaxillary bone is greater than that of the median nasal process (Inouye, '12). The portion of this bone that does not ossify in the median nasal process differentiates in the embryonic maxillary process (fig. 1). Hence the premaxillary bone ossifies in the unified connective tissue mass that results from the intimate fusion of the maxillary process with the median nasal process. This concept is accepted by all workers in the field, including Frazer ('40) and Keith ('48), who, however, confuse the matter by inferring that the labial (external) lamina of the premaxillary bone is derived only from the maxillary process.

A distinction should be made between the contributions of the embryonic membranous processes to the development of the adult lip and to development of the bones of the region.

Comparative anatomical studies by Boyd ('32) demonstrate that animals with definitive incisive sutures have many degrees of completely uncorrelated stages of the contributions of the medial nasal process to the formation of the upper lip and to the differentiation of the premaxillary and maxillary bones.

OSSEOUS MORPHOLOGY

The original investigations of Inouye ('12), Peter ('13), Felber ('17), and Chase ('42), are among the few papers in the literature concerned with this problem that present detailed observations made on 6 to 9 fetal week old human embryos. Their meticulous and critical studies are based on serial sections and wax reconstructions. These authors find no evidence of osseous overgrowth of the premaxillary bone by the maxillary bone (figs. 2 and 3). They insist that a process of fusion of the labial (external) lamina of the premaxillary bone with the analogous lamina of the maxillary bone occurs at about the 9th week and that thereafter evidence of this development process is irretrievably lost.

Our data support these views. Both the premaxillary bone and maxillary bone are present in each of our series of 15 embryos (bones stained with alizarin red) from 24 to 39 mm CR length (Noback and Robertson, '51). A 24 mm CR embryo has an incisive suture. In a 29 mm CR embryo, the right incisive suture is only present superiorly while the left suture is so narrow that the two bones are in contact. Evidences that the suture is being obliterated ectofacially are found in the other 13 embryos. Included are (1) the persistence of the upper third of the suture and (2) the presence of perforations in the lower two-thirds of the suture (fig. 3). The perforations, seldom found in older embryos, are interpreted as remnants of the suture. These morphological features may be found either unilaterally or bilaterally. No evidence is noted in our series to suggest that the medial ectofacial border of the maxillary bone is migrating medially over the premaxillary bone. Likewise an examination of 99 fetuses from 40 mm CR to 175 mm CR (up to 19 weeks

DL — dental lamina; IS — incisive suture; M — maxillary bone; MNP — medial nasal process; MP — maxillary process; N — primitive nasal cavity; PM — premaxillary bone; T — tongue.

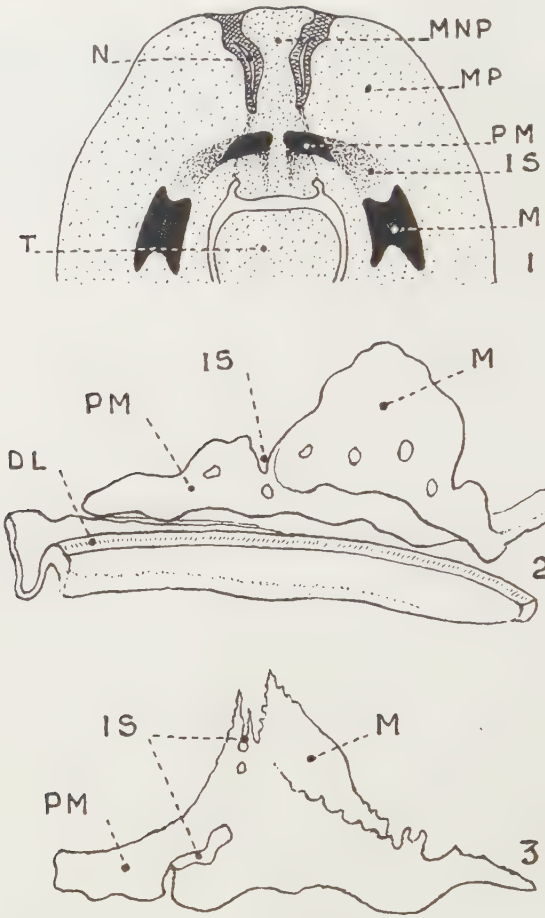

Fig. 1 Diagram illustrating the relation of the premaxillary bone and part of the maxillary bone to the medial nasal process and maxillary process in a 6–7 week old human embryo (after Inouye, '12). Note that each premaxillary bone ossifies in two embryonic processes — the medial nasal process and the maxillary process.

Fig. 2 Internal view of a wax reconstruction of the premaxillary bone, maxillary bone and dental lamina of a 7 week old human embryo (after Felber, '17). Note that the incisive suture is being obliterated by the fusion of the premaxillary bone and maxillary bone.

Fig. 3 External view of the premaxillary bone and maxillary bone from a 7 week old human embryo cleared and stained with alizarin red. Note that the incisive suture is being obliterated by the fusion of the premaxillary bone and the maxillary bone. No overgrowth of the premaxillary bone by the maxillary bone is observable.

of age) yields no evidence of the medial ectofacial overgrowth by the maxillary bone.

HISTORY OF THE PROBLEM

The European literaure and textbooks (Fischel, '29; DeBeer, '37; Brandt, '49) demonstrate that the premaxillary bone and the maxillary bone fuse ectofacially at the incisive suture. In addition they find no support for the overgrowth of the premaxillary bone by the maxillary bone. Chase ('42), in this country conclusively substantiates the fusion concept and rejects the overgrowth hypothesis. This paper escaped serious notice probably because of its publication in a dental journal.

In contrast, some of the British literature and textbooks confuse the picture by accepting the maxillary overgrowth concept without presenting evidence obtained from 6–9 week old human fetuses. The development of this thesis commenced with Callender (1868) and was subsequently expanded by Wood Jones ('29, '47), Frazer ('48), Johnson ('36), Keith ('48) and Woo ('49). It reached fruition in this country with the monograph of Ashley-Montagu ('35). Examination of Woo's ('49) figures — based on embryos from the correct temporal horizon — does not substantiate his claim of overgrowth. As recently as 1947, Wood Jones stated "Notwithstanding the numerous statements to the contrary, the suture between the maxilla and the premaxilla is never present on the human face at any pre- or post-natal stage." This statement, which has been disproven by several workers (vide supra), is at the root of the problem. The overgrowth school must produce evidence from direct observations taken at the proper time during embryonic growth period. If overgrowth does exist, evidence could be readily produced showing the medial migration of the maxillary bone in 6 to 9 week old human embryos.

CONCLUSIONS

1. Two schools exist concerning the fate of the premaxillary bone in man. One view holds that the maxillary bone

overgrows the ectofacial aspect of the premaxillary bone while the contrary view claims that the maxillary bone and premaxillary bone fuse ectofacially at the incisive suture.

2. The premaxillary bone and maxillary bone of man fuse at the ectofacial surface. This concept is supported by direct observations made on 6 to 9 week old human fetuses — the age during which the suture is obliterated. Data in the literature and original observations are presented.

3. Because a terminological confusion is present in some of the literature, it is essential to distinguish between the contribution of connective tissue processes and the osseous processes in this region.

4. The maxillary bone does not overgrow the ectofacial surface of the premaxillary bone. The overgrowth thesis is based on observations of fetuses over 9 weeks old — ages after which the incisive suture has been obliterated. No direct observations demonstrating the overgrowth have been presented in the literature.

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NEW METHOD OF SEX DETERMINATION. — We propose here a new index, which without pretending to solve the problem completely, appears to us to present advantages. It is the *acetabulo-sciatic index. . . .*

The two dimensions needed for this index are: (a) the distance from the edge of the acetabulum to the neighboring border of the sciatic notch; (b) the sciatic height, taken perpendicular from the same border to the postero-inferior iliac spine, where the internal border of the ilium joins the articular surface.

Since the sciatic height is usually greater in women than in men, and the acetabulo-sciatic distance less, the index b/a should reflect the sex difference.

We calculated this index in a series of innominates from mediaeval Geneva. The preliminary determination of sex was by eye, using the traditional characters. The series included 50 of each sex.

The average index, ignoring sex, was 122.8, with a range from 73.8 to 185.3. The male series had an average of 104.6, with range from 73.8 to 128.9; the female, an average of 141.0, with range from 92.5 to 185.3. The value 123 was set as an arbitrary limit, since only 6 (12%) of the males had a higher index, and 10 of the females (20%) had a lower index.— Marc-R. Sauter and François Privat. Une nouvelle méthode de détermination sexuelle de l'os coxal: l'indice cotylo-sciatique. Bull. Schweiz. Ges. f. Anthr. u. Ethnol., vol. 28 for 1951–52, pp. 12–13, 1952. (Abstract; freely translated.)

Eskimo Adaptation to Cold.— A comparative study on hand blood flow and temperature has been carried out on Eskimos in the Canadian Eastern Arctic and on medical students living in a temperate climate. One of the effects of chronic exposure of the individual to cold is a reduction in the ambient temperature required for comfort. At this low ambient temperature, the hand blood flow of the Eskimo is twice that of the white man and the skin temperature of his hand is greater. At any given water-bath temperature, the hand blood flow of the Eskimo is greater. The volume of the hand blood flow of the Eskimo changes more slowly in response to local cold. The degree of spontaneous fluctuation in hand blood flow is greater in the Eskimo and increases in both groups as the local temperature of the hand increases. The alterations which occur in the hand blood flow following chronic exposure to cold would appear to enhance hand function in the cold.— G. Malcolm Brown and John Page. The effect of chronic exposure to cold on temperature and blood flow of the hand. Journal of Applied Physiology, vol. 5, no. 5, November, 1952, pp. 221–227.

History of the Cohuna Cranium.— Anyone wishing to read a description of the Cohuna cranium must go to the daily press of the late 1920's and early 1930's, for no full description of it has ever appeared in scientific literature.

The cranium has passed through the hands of a succession of workers, each of whom intended making a description of it available to the scientific world, to the expressed approval and satisfaction of various authorities that this overdue task was about to be accomplished.

In a blast of press controversy, the cranium rocketed to fame in a brief period and was publicized as of brutal form and vast antiquity; but subsequently faded from the scene almost completely, being relegated to the class of anthropological bric-a-brac.

Curious too is the fact that, while disputing claims for its antiquity, the majority of scientific observers have been impressed on making its first acquaintance. . . .

The general morphological appearance is not very dissimilar from Talgai and Keilor, and the profile is like that of Talgai if allowance is made for Talgai's youth.

It lies nearer to the extreme limit of anatomical range presented by Talgai than does Keilor.— N. W. G. Macintosh. The Cohuna cranium: History and commentary from November, 1925, to November, 1951. Mankind, vol. 4, no. 8, March, 1952, pp. 307–329.

AN INVESTIGATION OF GENETIC VARIABILITY AMONG SUDANESE

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The Anglo-Egyptian Sudan covers an area of 967,500 square miles, ranging from approximately 22° to 4° N latitude, and from 22° to 36° E longitude. It is bounded on the north by Egypt; on the east by the Red Sea, Eritrea and Ethiopia; on the south by Uganda and the Belgian Congo; and on the west by French Equatorial Africa. Rainfall varies from none at the northern extreme to around 40 inches per year in the far south. Except for the Red Sea hills in the northeastern portion and the Nuba mountains in the west central region, the country is for the most part a vast plain. The northern portion of the Sudan is largely desert; the southern portion a savanna partially covered with acacia shrubs, and with tall grass in the rainy season. Vast swamps embrace areas on both sides of the White Nile and its tributaries during the rainy season.

The peoples of the Sudan fall into two distinct categories, both culturally and ethnically. The inhabitants of the northern portions are Mohammedan, speak Arabic for the most part, and are of mixed Arab and Negro descent. The inhabitants of the southern Sudan are Pagans, each major tribe having its own language and culture. The people here are essentially Negroid, and may be classified into three major groups as follows: (1) Sudanic, various groups of tribes west of the White Nile (Nuba, Azande); (2) Nilotes (Nuer, Dinka, Shilluk); (3) Nilo-Hamites (Bari, Lotuka, Lango).

Seligman ('32), in company with many other anthropologists, was convinced that for the most part these groups are

not pure Negro, but have mixed in times past with Hamitic peoples who invaded the region. This belief is based upon linguistic evidence, cultural practices, and the occasional occurrence of typically Hamitic features among these peoples.

The Nilotes occupy the swamp region on either side of the White Nile from 7°30′ N and extend south to within 120 miles of the Uganda border. In 1952 the number of Nilotes was estimated to be approximately one and one-third million (Sudan Almanac, '52). They are characterized by tall stature, dolicocephaly, long slender legs, and very dark pigmentation.

The Nilo-Hamites inhabit the extreme southern portions of the Sudan, along both sides of the river, and their population is estimated at 100,000. They are typically mesocephalic and not quite as tall as Nilotes.

The Sudanic tribes, according to Seligman ('32), show less evidence of Hamitic mixture than do either the Nilotes or the Nilo-Hamites. They have a population estimated to number 230,000.

This paper is concerned with the findings of a recent investigation [1] of the incidence of certain common genetic variations among 6 Sudanese populations. The samples which were tested included 132 Dinka, 110 Nuer, 105 Shilluk, 72 Bari, 100 mixed northern Sudanese, and 51 college students from various parts of the Sudan. Data, taken on males only, included the ABO blood groups, palm and finger prints, taste reaction to phenyl-thio-carbamide, handedness and kodachrome photographs. Data on the three Nilotic tribes were obtained at Malakal, a native village about 500 miles south of Khartoum along the White Nile. Persons tested included inmates of the government prison, workers at the experimental farm, and out-patients at the hospital. All three tribes were represented at each of these places. Data from Bari were obtained at Khartoum from young men who had come from their homes

[1] These data were collected during February, 1952, by an expedition consisting of Dr. and Mrs. E. T. Bullard, Mr. Robert Murphy, Mr. Martin Johnson, Mr. Rafai Bayoumi, and the author. All members of the expedition, with the exception of Mister Bayoumi, were at that time holders of Fulbright Awards to Egypt.

in the southern Sudan to work temporarily as servants. Farouk Secondary School in Khartoum provided a sample of 100 northern Sudanese, while University College provided 51 students, from various parts of the Sudan.

Grateful acknowledgment is due to the following institutions and individuals, without whose excellent cooperation and support the project could not have been completed: the United States Educational Foundation for Egypt, The Sudan Agency in Cairo, The Sudan Government, The Faculty of Science at Fouad I University in Cairo, Governor Longe of the Upper Nile Province in the Sudan, Mr. Mohammed S. Roda (Controller of Egyptian Education in the Sudan), Doctor Sandon of University College in Khartoum, and Father Vantini of the Catholic Mission in Khartoum.

RESULTS

Blood groups

The ABO blood groupings of 312 Shilluks, Dinkas, and Nuers were determined, and the results are shown in table 1. Of the three tribes the Nuers and Dinkas show striking similarities, while the Shilluks show a higher frequency of gene I^B, and a lower frequency of I^A. Although suggestive, the differences between the Shilluks and the others are statistically insignificant.

Corkill ('49) investigated the ABO blood groups of over 4,370 Sudanese soldiers, some of his results being shown in table 1. Most of them were from northern and north central tribes, the only Nilotes being 56 Dinkas. The table shows the distribution of the blood groups among typical northern Arab tribes (Riverain), a negro tribe (the Nuba), and the Dinka. Note that the Dinka tested by Corkill show close similarities to our own sample, and that the other two tribes have much the same distributions.

TABLE 1

Observed frequencies of the ABO blood groups among Sudanese and other populations

POPULATION	INVESTIGATOR	NUMBER OF INDIVIDUALS	%O	%A	%B	%AB	p	q	r
Shilluk	Rife et al.	91	52.75	19.78	24.17	3.30	.125	.151	.726
Nuer	Rife et al.	100	52.00	28.00	17.00	3.00	.173	.109	.721
Dinka	Rife et al.	121	52.89	28.09	14.87	4.13	.172	.096	.727
Riverain Arabs	Corkill	598	45.00	27.00	25.00	3.00	.178	.166	.670
Nuba	Corkill	380	45.00	34.00	17.00	4.00	.219	.117	.670
Dinka	Corkill	56	49.00	28.00	14.00	9.00	.177	.093	.700
Total of Sudanese soldiers (mostly northern)	Corkill	4,370	45.40	27.80	22.20	4.50	.194	.149	.673
Egyptians	Abdoosh and El-Dewi	10,045	32.60	35.40	24.30	7.45	.282	.184	.571
Congo Negroes	Bruynoghe and Walravens (After Wiener)	500	45.60	22.20	24.20	8.00	.165	.177	.675
West African Negroes	Lewis and Henderson (After Wiener)	325	52.30	21.50	23.00	3.20	.133	.143	.724
Arabs (Syria)	Boyd	208	43.30	22.10	30.30	4.30	.151	.200	.658

It is also of interest to compare the Sudanese with their peoples of neighboring countries. Table 1 includes the blood groups of Egyptians, West African Negroes, and Congo Negroes. It is readily apparent that both northern and southern Sudanese are quite similar to the Negroes of both the Congo and western Africa. Nilotic Negroes differ in having slightly lower percentages of I^B, but the general pattern is much the same. They differ greatly from Egyptians, especially in having a much higher frequency of gene *i*. It would be of interest to compare Arabs from Arabia with the Sudanese, but unfortunately such data are as yet unavailable. The rather close resemblance of northern with southern Sudanese suggests a predominance of Negro ancestry among the northern Sudanese.

Dermatoglyphics

Handprints were obtained from all 6 populations investigated. Table 2 shows the percentages of whorls, loops, and arches on the finger-tips of each. All three Nilotic tribes are characterized by relatively low frequencies of whorls, from 25% to 28%. Bari shows slightly higher frequencies, University College students around 35% whorls, whereas the northern Sudanese from Farouk School have the highest frequencies of all, almost 46%. It is quite evident that northern Sudanese have significantly higher frequencies of whorls than the southern Sudanese. They are similar to the pattern frequencies of Arab peoples who have been investigated (Cummins and Shanklin, '37). Unfortunately, no data are available on the dermatoglyphics of Arabs from Arabia. The pattern values of the southern Sudanese are quite similar to those from West Africa (table 5). Mixed Sudanese show intermediate pattern values which might be expected in view of the fact that they represent all portions of the Sudan.

Table 3 shows the incidence of palmar patterns. Here again southern Sudanese present similarities to Negroes in other parts of the world, in that they are characterized by high pattern frequencies in the 4th interdigital area, and low

ones in the third interdigital area. Frequencies of second interdigital patterns and thenar/first interdigital patterns are lower than in some Negroes, while the frequencies of patterns in the hypothenar area are low, corresponding with other Negro populations. Here the northern Sudanese from Farouk

TABLE 2

Observed frequencies of patterns on finger tips among Sudanese populations

POPULATION	NUMBER OF INDIVIDUALS		% WHORLS	% LOOPS	% ARCHES
Northern Sudanese (Farouk School)	100	Right	45.29	51.30	3.01
		Left	46.57	48.98	4.45
		Total	45.93	50.34	3.73
Mixed Sudanese (University College Khartoum)	50	Right	36.69	60.51	2.80
		Left	35.20	61.60	3.20
		Total	35.94	61.06	3.00
Bari	72	Right	32.29	63.27	4.44
		Left	32.60	62.13	5.27
		Total	32.44	62.71	4.85
Shilluk	106	Right	29.34	68.48	2.18
		Left	23.72	72.17	4.11
		Total	26.53	70.32	3.15
Dinka	132	Right	30.40	65.44	4.16
		Left	25.90	68.14	5.96
		Total	28.15	66.79	5.06
Nuer	110	Right	25.04	69.46	5.50
		Left	24.86	67.78	7.36
		Total	24.95	68.62	6.43

Secondary School show another marked contrast in the hypothenar area, where patterns are almost twice as abundant as in the southern Sudanese. There are no outstanding differences in any of the other areas, although patterns occur a little less frequently in the 4th, and more frequently in the third interdigital areas. Here again, mixed Sudanese show frequencies between those of northern and southern Sudanese students.

Table 4 shows the frequencies of 11.9.7., 9.7.5., and 7.5.5. main line formulae among the 6 populations. It is quite evident that the northern Sudanese possess higher main line values than

TABLE 3

Observed frequencies of palmar patterns[1] *among Sudanese populations*

POPULATION	NUMBER		HYPOTHENAR	THENAR/FIRST INTERDIGITAL	SECOND INTERDIGITAL	THIRD INTERDIGITAL	FOURTH INTERDIGITAL
			%	%	%	%	%
Northern Sudanese	100	Right	28.00	6.00	12.00	48.00	56.00
		Left	27.00	18.00	5.00	22.00	75.00
		Total	27.50	12.00	8.50	35.00	65.50
Mixed Sudanese	50	Right	42.00	4.00	10.00	40.00	56.00
		Left	32.00	8.00	8.00	30.00	76.00
		Total	37.00	6.00	9.00	35.00	66.00
Bari	72	Right	16.52	6.94	8.05	61.11	76.38
		Left	16.52	16.52	6.26	33.33	81.94
		Total	16.52	11.80	7.16	47.22	79.16
Shilluk	106	Right	15.09	6.60	16.50	43.56	67.32
		Left	14.15	20.75	4.76	19.60	77.64
		Total	14.62	13.67	10.63	31.58	72.48
Dinka	132	Right	15.15	2.27	15.90	40.00	66.92
		Left	10.60	15.90	6.81	18.32	80.52
		Total	12.87	9.08	11.35	29.16	73.78
Nuer	110	Right	9.18	4.59	13.77	39.25	57.94
		Left	8.18	27.27	9.09	20.90	79.09
		Total	8.68	11.43	11.35	30.08	68.51

[1] Palmar patterns consist of whorls and loops. The hypothenar area is on the ulnar side, the thenar/first interdigital area is on the radial side, and the second, third and fourth interdigital areas are located on the distal portion of the palm. The second interdigital area is located below the index and middle fingers, the third interdigital area below the middle and ring fingers, and the fourth interdigital area below the ring and little fingers.

do any of the other populations, while mixed Sudanese possess values intermediate between those of northern and southern Sudanese.

Taken as a whole, northern Sudanese manifest rather close similarities to Arabs, whereas the prints of southern Sudanese resemble those of Negroes in other parts of the world (table

5). The contrasts between northern and southern Sudanese with respect to the incidence of patterns on fingers and the hypothenar area of palms, and main line formulae are highly significant. It is of interest to note that differences in dermatoglyphics are much greater than those in the ABO blood

TABLE 4

Incidence of various palmar main line formulae [1] *among Sudanese populations*

POPULATION	SIDE	11.9.7.	9.7.5.	7.5.5.	OTHERS	NUMBER PALMS
		%	%	%	%	
Northern Sudanese	Right	30.00	12.00	6.00	52.00	100
	Left	7.00	17.00	16.00	60.00	100
Mixed Sudanese	Right	26.00	20.00	16.00	62.00	50
	Left	8.00	14.00	28.00	48.00	50
Bari	Right	19.44	5.55	16.05	58.96	72
	Left	4.22	7.04	26.76	62.98	71
Shilluk	Right	17.17	13.13	21.21	48.49	99
	Left	3.96	20.70	22.77	47.39	101
Dinka	Right	21.70	17.05	24.31	34.94	130
	Left	3.84	13.05	23.84	59.27	129
Nuer	Right	20.56	8.41	21.49	49.54	107
	Left	6.42	16.51	21.00	56.07	109

[1] Main line formulae provide a criterion for the degree of transverseness of palmar ridges. The higher the numbers in the formula, the greater the transverseness. Thus a formula of 11.9.7. indicates greater transversality than does 7.5.3.

groups. It should be remembered in this connection that different groups of northern Sudanese were represented in the data for these traits; in fact the soldiers whose blood was tested were not all northern Sudanese, whereas the dermatoglyphics were obtained from a population all of whose members were known to be from the north.

Taste reaction

Ability to taste phenyl-thio-carbamide was tested by placing a small amount of the substance on a toothpick and ap-

TABLE 5

Frequencies of palm and finger-tip dermatoglyphic configurations among various populations

POPULATION	INVESTIGATOR	NUMBER HANDS	WHORLS	HYPOTHENAR	THENAR/FIRST INTERDIGITAL	SECOND INTERDIGITAL	THIRD INTERDIGITAL	FOURTH INTERDIGITAL		MAIN LINE FORMULAE 11.9.7.	9.7.5.	7.5.5.
			%	%	%	%	%	%		%	%	%
West African Negroes	Cummins	104-200 [1]	38.9	18.2	15.7	9.8	29.6	89.2	R.	17.3	17.3	34.6
	Dankmeijer	476	29.2						L.	2.5	26.2	55.0
Jamaican Negroes	Davenport and Steggerda	134	29.4	20.1	14.9	9.7	35.7	87.2	R.	17.9	10.4	20.8
									L.	10.4	7.4	33.9
American Negroes	Rife	86	25.9	30.2	17.4	16.2	39.5	79.0		...	...	...
Rwala Bedouins (Syria)	Shanklin and Cummins	400	39.1	35.4	8.3	5.7	37.9	56.9		...	...	...
American Jews	Rife	756	38.8	35.1	11.7	8.2	47.7	66.3		...	...	...

[1] As prints of some palms were partially illegible, the number of those available for recording varied between the above figures.

plying it on the back of the tongue. If no taste reaction was reported after a minute the individual was classified as a non-taster. If a distinct taste reaction was experienced, the individual was classed as a taster. Table 6 shows the percentages of tasters observed in each of the Sudanese populations which were investigated. The highest frequencies were found among the northern Sudanese, the lowest among the Dinka.

The data on the northern and the mixed Sudanese are undoubtedly more reliable than that obtained from the southern Sudanese tribes, as the former could speak English, whereas each of the 4 Sudanese tribes spoke only their tribal language.

TABLE 6

Observed frequencies of tasters of phenyl-thio-carbamide among Sudanese populations

POPULATION	NUMBER TESTED	% TASTERS	p	q
Northern Sudanese	100	96.00	.800	.200
Mixed Sudanese	51	82.36	.580	.420
Bari	70	92.86	.733	.267
Shilluk	105	80.00	.533	.447
Dinka	132	65.16	.410	.590
Nuer	110	81.82	.574	.426

It was therefore necessary to depend upon native interpreters for the Shilluk, Nuer, Dinka, and Bari in order to record their reactions. The percentages of tasters among the three Nilotic groups, especially the Dinka, are lower than noted among Negroes by other investigators. The suspicion that data from the southern Sudanese might not be altogether reliable was strengthened by the observation that the prisoners in all three Nilotic tribes showed significantly lower percentages of tasters than did the non-prisoners (see table 7).

These differences are highly significant and consistent in each of the three tribes. The blood groups and dermatoglyphics of the prisoners and non-prisoner groups were compared and no significant differences were found, nor were any real

differences even suggested. Apparently the discrepancies between prisoners and non-prisoners are not due to sampling errors. It is conceivable that there may be some biological correlation between criminal tendencies and ability to taste phenyl-thio-carbamide, but this seems highly improbable. The most logical interpretation seems to be that some people who were not tasters were not fully aware of the nature and purpose of the test.

TABLE 7

Observed frequencies of tasters of phenyl-thio-carbamide among three Nilotic tribes, classified as prisoners and non-prisoners

TRIBE	PRISONERS		NON-PRISONERS	
	Number	% Tasters	Number	% Tasters
Shilluk	40	66.87	65	86.17
Dinka	86	55.82	46	76.09
Nuer	32	62.50	78	89.75
	df = 2	$P < .01$	$\chi^2 = 28.61$	

TABLE 8

Observed frequencies of left-handedness among Sudanese populations

POPULATION	NUMBER TESTED	% LEFT-HANDEDNESS
Northern Sudanese	100	2.00
Mixed Sudanese	51	3.92
Bari	70	1.43
Shilluk	105	6.67
Dinka	132	6.06
Nuer	110	5.45

Handedness

Inquiry was made of all persons tested as to the preferred in hand in throwing and use of a spear. Observations were recorded of the hand used in writing by the northern and mixed Sudanese, but such observations could not be made concerning the illiterate southern Sudanese tribes. None of those tested showed evidence of mixed handedness. Table 8 shows the observed frequencies of lefthanders in the 6

population samples. The Nilotes manifest approximately 6% of left-handedness, more than any of the other three groups. Although suggestive, too little is known as yet concerning the frequencies of left-handedness among ethnic groups to shed much light on the genetic relationships of northern and southern Sudanese with each other, and with the peoples in neighboring countries.

DISCUSSION

Both the ABO blood group and the handprint data obtained from the Nilotes indicate close relationship with Negroes from other parts of Africa. Northern and southern Sudanese show similar blood group distributions, but differ markedly from Egyptians. The dermatoglyphics of northern Sudanese show significant differences from the southern Sudanese, and in many respects resemble those of Arabs and other Semitic people. Of the 4 traits compared, dermatoglyphics present the most objective data of all. The records are permanent and are products of polygenic interactions, modified to a minor degree by environmental conditions *in utero*. Because of their polygenic nature, they are less subject to chance fluctuations in their frequencies than are the various blood groups, each of which appears to owe its variations to multiple alleles. Unfortunately, the unique advantages of dermatoglyphics as a tool in human population studies have frequently been overlooked by anthropologists and geneticists. The ABO blood groups are, of course, far more objective than tasting ability and handedness.

The ABO blood groups and the dermatoglyphics of the Nilotes do not present evidence supporting the popular belief that they have considerable Hamitic ancestry. Moreover, they appear, almost without exception, to possess dark brown or blackish skin and woolly hair. If they have Caucasian ancestry, we should expect to find segregation of lighter skin and non-woolly hair. Even Seligman ('32) who is convinced of Hamitic ancestry among the Nilotes states: "Yet, strangely enough, it is these mixed tribes that exhibit the darkest skins,

and, in spite of the moderate stature of most Hamites, the tallest stature."

The languages and cultures of the Nilotes and Nilo-Hamites present unmistakable evidene of close contact with Hamites at some time in the past, but do not necessarily imply extensive interbreeding. Nor does the occasional appearance of atypical features necessarily prove interbreeding with non-Negroid peoples. Recurrent and parallel mutations could account for many physical similarities between different ethnic groups.

The three types of southern Sudanese (Nilotes, Nilo-Hamites, Sudanic) appear to be essentially Negroes, differing from each other with respect to the frequencies of variations in such traits as stature and head shape. These inter-group differences are of the same order as those encountered among European populations. The genetic data do not support the belief that the Nilotes and Nilo-Hamites have a substantial proportion of Hamitic ancestry.

SUMMARY

1. The ABO blood group distributions and hand prints of Nilotes and Nilo-Hamites show close resemblances to each other and to Negroes in other parts of the world.

2. The ABO blood group distributions of northern Sudanese are similar to those of the Nilotes, but differ markedly from those of Egyptians.

3. The dermatoglyphics of northern Sudanese show several outstanding differences from the Nilotes and Nilo-Hamites, and also show many resemblances to Arabs and other Semitic people.

4. The genetic data clearly indicate mixed Negro-White ancestry of the northern Sudanese.

5. The genetic data indicate that the southern Sudanese are essentially Negroid, rather than of mixed Negro-White descent.

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A COMPARATIVE ANALYSIS OF THE DIGITAL PATTERNS OF ESKIMO FROM SOUTHAMPTON ISLAND

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The pioneer study of Eskimo dermatoglyphics, based upon a series of prints collected on St. Lawrence Island, was reported by Midlo and Cummins in 1931. Up to the present, descriptions of only 4 additional samples from localities in Alaska, Greenland and the eastern Canadian Arctic have appeared in the literature. Although these data are inadequate for a definitive analysis of dermatoglyphic variation among the Eskimo, some evaluation of the available material would seem to be useful at this time, to point out certain of the lacunae in this field of Eskimo research and provide suggestions for future investigation. Consequently, when a series of prints from Southampton Island recently became available for study, it was decided to attempt such an evaluation in conjunction with a description of the new material. Attention was confined to digital patterns since, among other considerations, only data of this type were common to all reports on the Eskimo. However, it has been pointed out that digital patterns are probably under more rigid genetic control than other dermatoglyphics and therefore are more useful for studies of racial variation. Further, some correlation exists between expressions of patterns in different areas. Thus it may be expected that plantar and palmar trends will follow in a general way those established for finger patterns (Cummins and Midlo, '43).

THE SOUTHAMPTON ISLAND SERIES

Palm and finger impressions of 78 Eskimo were obtained by Jamieson Bond during the summer of 1950 while engaged in an ethnographic study, sponsored by the Arctic Institute of North America, and under the direction of Dr. E. S. Carpenter of the University of Toronto.[1] Bond took special pains to discover the presence of non-Eskimo elements in his subjects and marked as "mixed" the prints of those individuals whose reported ancestry indicated racial admixture or who were suspect on phenotypic grounds. Of 16 cases in this group, 14 were Aivilik among whom a great deal of European admixture has taken place. Concentrations of relatives in the sample appear to be at a minimum; so far as could be ascertained from the names and kinship data given with the prints, the 62 "pure" Eskimo were distributed among 38 families. However, since there was about 40% adoption among the Eskimo of at least one group (Aivilik) living on the Island, it cannot be stated with certainty to what extent these are social or biological families.

The approximate Eskimo population of Southampton Island in 1950 was 225. Most of these or their immediate forbears migrated to the Island from surrounding areas at various times during the past 25 years. The series studied comprised 20 Aivilik from Repulse Bay, 20 Okomiut from Cumberland Sound and 22 Kidlinikmiut (including Akianimiut) from Port Burwell and Cape Chidley on the south coast of Hudson Strait.

Conventional standards were employed for the diagnosis of digital patterns; lateral and central pocket and double loops were classified as whorls, and "loops" with zero ridge counts as arches (Cummins and Midlo, '43). The frequencies of the 4 principal pattern types are recorded by finger and hand for

[1] The Southampton Island prints are now in file in the Department of Zoology, University of Toronto, and were made available through the kindness of Dr. Norma Ford Walker, to whom the writer is also deeply indebted for valuable suggestions in the course of this study. Grateful acknowledgment is also due Dr. E. S. Carpenter of the Department of Anthropology, University of Toronto, for a critical reading of the manuscript.

each sex in table 1. These apply only to the 62 Eskimo (28 males and 34 females) in whose ancestry there was no evidence of racial admixture.

It is noteworthy that the mixed group, who are chiefly Aivilik with some degree of European ancestry, are characterized by a remarkably high proportion of arches (9.4%) and a compensatory reduction in the frequency of whorls (35.9%). This distribution of digital patterns may be contrasted with that of the unmixed Aivilik sample among whom whorls occur as the most common pattern (49.4%), and arches are relatively

TABLE 1

Frequencies of digital patterns among 28 male and 34 female Eskimo from Southampton Island

		I		II		III		IV		V		TOTAL
		R	L	R	L	R	L	R	L	R	L	
Arch	M	0	0	1	2	0	1	0	0	1	1	6
	F	1	1	4	3	1	3	1	1	2	5	22
Ulnar loop	M	8	12	13	14	21	19	11	14	20	20	152
	F	9	15	7	9	26	18	13	10	26	23	156
Radial loop	M	0	1	3	3	0	0	0	0	0	0	7
	F	0	0	3	4	0	0	0	0	0	0	7
Whorl	M	20	14	11	7	6	7	17	14	7	7	110
	F	24	18	19	18	7	13	20	23	6	6	154

infrequent (3.1%). The trend in general is in the European direction; the pattern intensity index of 12.7 falls within the European range (Cummins and Midlo, '43, p. 260). A similar trend is evident in Abel's ('33) series of 14 "Dane-Eskimo hybrids," for whom 5% arches, 34.2% whorls and a pattern intensity index of 12.9 were reported.

The chi-square technique was employed to test the homogeneity of the 62 "pure" Eskimo in the sample. A contingency table containing the absolute frequencies of arches, whorls and loops (radial and ulnar combined) in each of the three groups, Aivilik, Okomiut and Kidlinikmiut, was constructed. A chi-square of 17.1 with 4° of freedom was ob-

tained indicating a significant difference ($P<.01>.001$). This difference was apparently introduced largely by a relatively high incidence of arches among the Okomiut. Since the numbers of patterns involved were quite small, it was decided to overlook this lack of agreement and assume an homogeneous sample of 62. Future studies may prove this assumption to have been incorrect. Indeed, a number of observers have pointed out that the Okomiut appear distinct physically from other Eskimo presently living on Southampton Island. Nevertheless, the samples are too small to provide adequate justification for the separation of the Okomiut on dermatoglyphic evidence. The question of homogeneity in dermatoglyphic samples will be discussed further in the section on comparative data.

SEXUAL DIFFERENCES

Dankmeijer ('38) has reported a consistently higher incidence of arches as a female characteristic. This was observed in the present sample; the proportion of arches in females (6.5%) was nearly three times that in males (2.2%). However, the increase in arch frequency was accompanied by a reduction in number of loops rather than in whorls. The proportion of the latter was slightly higher in the female sample (♀ : 45.4%; ♂ : 40%). Cummins and Hansen ('46) recorded a similar absence of the commonly observed sex differential of more whorls in males in their west Greenland series. A difference was also noted in the type of symmetry exhibited by the distribution of digital patterns in males and females. It may be recalled that Poll ('38) described two different forms of dactyloglyphic symmetry which he termed the pair-group rule and the rule of all pairs. He suggested the possibility that a sex difference might be present in some populations, but the studies available to him were either based on too little data or the sexes had not been separately analyzed. Among Eskimo studies, Cummins and Hansen ('46) have reported that the trend toward the rule of all pairs in their west Greenland series was introduced by the females.

Auer ('50), working with large numbers of each sex, was able to demonstrate that the rule of all pairs held for females and the pair-group rule for males. In the Southampton Island sample, the rule of all pairs seemed quite definitely to hold for the females and not for the males. However, neither rule could be clearly defined in the male group, probably because the sample was too small, but the trend appeared to be in the direction of the pair-group form of symmetry.

COMPARATIVE DATA

The reliability of the Eskimo data available for comparative study may be evaluated in terms of 4 criteria, namely, degree of racial admixture, concentrations of related individuals, analytical differentiation of the sexes, and homogeneity.

There appears to have been a strong tendency to minimize the factor of racial admixture in the Eskimo samples which have been described. Some persons of mixed ancestry seem to have been included in every instance but this is a largely unavoidable circumstance. The inclusion of related persons has also occurred to some extent in all samples but appears to be minimal except in the case of Abel's east Greenland Eskimo ('33). This series has been rendered unreliable for comparative study because of extreme over-concentration of members of the same families, which has considerably distorted the dermatoglyphic picture. Separate analyses of the sexes have been undertaken only by Auer ('50) and less fully by Cummins and Hansen ('46). It is therefore necessary to employ the figures based upon combined samples for comparative purposes. The effect of this is difficult to assess. It is possible that the sex differences in digital pattern frequencies which are known to exist (Dankmeijer, '38) are more or less constant within a given population or racial group. If this should prove to be so, and provided the sexes were about equally represented, the use of pattern frequencies based upon mixed samples should not unduly obscure any significant intra-racial variations which might be present. Among the various series considered in the present study, the only se-

rious departure from a one-to-one sex ratio may have occurred in the Point Barrow sample (Cummins, '35) which comprised 16 females and 39 males. However, finger print sets were not available for all of these and Cummins' analysis was based upon the 30 individuals for whom complete data were available; the sex ratio in this group was not reported.

The final criterion to be considered concerns the homogeneity of the sample. The degree of homogeneity present depends upon the extent to which members of divers genetic isolates have been pooled in a sample under the assumption that, since all were Eskimo in a broad ethnographic sense, all had been selected from the same dermatoglyphic population. The three samples from Point Barrow, St. Lawrence Island and southwest Greenland, reported by Cummins and his associates, represent small, geographically restricted populations and therefore probably can be regarded as homogeneous series in this sense. On the other hand, Auer's ('50) prints were obtained from Eskimo living as far apart as Eskimo Point on the west coast of Hudson Bay and Ellesmere Island in the extreme northern Arctic. Judging by the localities given, Aivilik and Okomiut were almost certainly included and there were probably also Aggomiut in the sample. Since the digital pattern frequencies reported for this series differ significantly from those in Eskimo from St. Lawrence Island, Point Barrow, Southampton Island and southwest Greenland, the possibility that more than one dermatoglyphic population were represented becomes especially important. As already pointed out, the Southampton Island series is also heterogeneous from an ethnographic point of view and probably has in common with Auer's sample the presence of Aivilik and Okomiut. Nevertheless, the two groups differ in pattern frequencies, the Southampton series agreeing well with the St. Lawrence Island, Point Barrow and southwest Greenland and Auer's group being divergent. Evidently a majority of the prints used by Auer were obtained on north Baffin Island so that the differences may indicate the existence of a local dermatoglyphic variant living in this area. However, a precise

definition of this variation, if it exists, is precluded by the fact that separate analysis of the sub-samples in the series, which would have provided a test of homogeneity, was not reported.

Indices and percentage occurrence of digital patterns in the combined Southampton Island series and the 5 Eskimo samples which have been described in the literature to date are given in table 2. The numbers of patterns upon which these proportions are based have been included since the statistical analysis which follows was based on these and there was not always agreement between the number of individuals in the sample and the number of patterns used in the analysis. By way of providing a broader perspective, the figures for a sample of Pekangecum Saulteaux, based upon prints of 55 males and 46 females, have been included. These Indians live in the neighborhood of Lake Pekangecum, Ontario, near the Manitoba border, and are among the least acculturated of Algonkian peoples. No known European intermarriage has occurred in the ancestry of the individuals included in the sample (Walker, '50).

A comparison of these series (omitting Abel's east Greenland Eskimo) was conducted by means of the chi-square technique. The 4 groups which appeared most similar on the basis of gross proportions were compared first. These were the Southampton Island, Point Barrow, St. Lawrence Island and southwest Greenland samples. The absolute frequencies of arches, loops and whorls were compared in a three by 4 contingency table on the assumption that if the 4 groups were independent samples of the same dermatoglyphic population, the differences would not be significant. A chi square of 7.98 with 6° of freedom was obtained for these data. The differences were therefore not significant ($P<.30>.20$) and the hypothesis that all 4 samples represent the same dermatoglyphic population may be accepted. When the frequencies for Auer's east-central Arctic series were introduced and chi square was recalculated, an highly significant difference was obtained ($P<.001$). Auer's sample is characterized by a

marked increase in the incidence of ulnar loops entirely at the expense of whorls. Indeed, the whorl frequency of these Eskimo is nearly 10% below that of most Eskimo, North American Indian and Asiatic Mongoloid populations (Cummins and Midlo, '43, p. 260). The digital pattern frequencies of the Saulteaux Indians differed significantly from those of

TABLE 2

Indices and per cent frequencies of digital patterns in Southampton Island Eskimo and comparative series

	NO. OF PATTERNS	ARCH	R. LOOP	U. LOOP	WHORL	INDEX OF PAT. INT.	% ARCH × 100 / % WHORL
Southampton Island	614	4.6	2.3	50.2	43.0	13.8	10.7
West Greenland (Cummins and Hansen, '46)	1400	3.5	3.6	50.5	42.5	14.0	8.2
Point Barrow (Cummins, '35)	300	2.3	2.3	49.0	46.3	14.4	5.0
St. Lawrence Isl. (Midlo and Cummins, '31)	590	4.4	1.9	46.9	46.8	14.2	9.4
East-Central Arctic (Auer, '50)	4607 [1]	2.9	3.1	59.6	34.4	13.2	8.6
East Greenland (Abel, '33)	680	0.8	0.7	26.2	72.2	17.3	1.1
Saulteaux Indians (Walker, '50) [2]	1009	2.0	3.3	37.3	57.4	15.5	3.5

[1] Auer's sample comprised 452 individuals so that 4,520 patterns is the maximum possible. This discrepancy is not explained in his report; the error appears to lie in the counts for females. The frequencies recorded by Auer have been employed in the present analysis.

[2] Unpublished data.

the Eskimo samples. The Indian group featured a much increased whorl frequency with compensatory reduction in the incidence of ulnar loops.

DISCUSSION

Perhaps the most interesting outcome of the comparative analysis which has been presented, is the apparent similarity in digital pattern frequencies among such widely separated Eskimo peoples as those from St. Lawrence Island, Point Barrow, Southampton Island and southwest Greenland. Physical similarities among other geographically disparate Eskimo groups have been reported in anthropometric studies. Hrdlička ('10), for example, in a study of Sadlermiut crania from Southampton Island, pointed out that, "Taking everything into consideration . . . the Southampton Island crania approximate the more Western, particularly Alaskan, rather than the more Eastern Eskimo" (p. 183). The same author ('30) stressed the resemblance between south Greenland and Old Igloo crania from Barrow, Alaska. Shapiro ('31), working with measurements of the living, concluded that, "the Smith Sound Eskimo with those from Coronation Gulf and with our sample from Seward Peninsula . . . form a unit stretching from northwestern Greenland to Alaska" (p. 376). Unfortunately, it is not yet possible to determine adequately whether or not our "trans-Arctic" similarity in digital pattern frequencies is strictly analogous to these findings, since insufficient anthropometric data exist for those Eskimo whose dermatoglyphic characteristics have been described. Further dermatoglyphic data which can be correlated with satisfactory anthropometric information are required. This would make possible an evaluation of the extent to which known physical variations among the Eskimo, which have been defined anthropometrically, are also differentiated by dermatoglyphic characteristics. Specifically, the groups which should receive attention from this point of view are Labrador Eskimo, Polar Eskimo from the region of Smith Sound, Copper and Macken-

zie Eskimo, and Alaskan Eskimo of the Noatak River and Seward Peninsula areas in the northwest and the Kuskokwim Basin in the southwest. Finally, further attention might be profitably given to the Eskimo of Baffin Island, particularly the Aggomiut and Okomiut, with a view to establishing or rejecting the possibility of a distinctive dermatoglyphic variant in this region.

SUMMARY

Analysis of 614 digital impressions of 62 Eskimo from Southampton Island indicated 4.6% arches, 2.3% radial loops, 50.2% ulnar loops and 43% whorls. A much higher arch frequency and slightly higher whorl frequency were observed in females. Symmetry analysis revealed a clearly defined rule of all pairs in females and indications of the pair-group relationship in males. An additional sample of 16 individuals of mixed ancestry exhibited a European trend with increase in arch and decrease in whorl frequency.

Comparison by means of the chi-square test revealed statistical agreement in digital pattern frequencies of St. Lawrence Island, Point Barrow, Southampton Island and southwest Greenland Eskimo and significant divergence of an east-central Arctic sample. Precise definition of this divergence was precluded because the sample comprised Eskimo from geographically disparate groups and a comparison of these, as a test of homogeneity, had not been reported. All Eskimo series differed significantly from a sample of Pekangecum Saulteaux characterized by much higher whorl and reduced loop frequencies.

Since little is known of the extent to which local variations are reflected in dermatoglyphic characteristics, it is difficult to assess the significance of similarities between widely separated Eskimo populations. A step in this direction might be made if dermatoglyphic data were available for Eskimo groups known to differ on anthropometric grounds.

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SUPPLEMENTARY DATA ON AUSTRALOPITHECINES.— One of the problems at present facing students of the australopithecines and their associated fauna is the uncertainty regarding the geological age of the deposits in which these specimens occur. . . .

While much has been published about specimens obtained from excavations, little has been written about the excavations as such. . . .

The geology and faunal composition of the sites in the Sterkfontein area suggests that their histories have not been exactly the same nor are they contemporaneous. The hypothesis that the ape-men lived in an arid epoch, in which the Sterkfontein area was invaded either by the Kalahari or a Kalahari type of environment, does not seem to be supported by the geological and faunal evidence. On the contrary, the evidence seems to indicate that the climate differed little from that of the present day. The difficulty in arriving at an absolute age for the sites is increased by the fact that there is no sharp transition, in South Africa, from Pliocene to Pleistocene. If such is present, we do not yet know enough about the geology and faunal history to be able to detect it. What little evidence there is seems to point to an Upper Pliocene date.— J. T. Robinson. The australopithecine-bearing deposits of the Sterkfontein area. Annals, Transvaal Museum, vol. 22, pt. 1, November 4, 1952, pp. 1–19. (Includes detailed description of Swartkrans site.)

HEMAGGLUTINOGENS OF THE CHIMPANZEE

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In a previous report, the author (Butts, '50) described a new human blood factor which was detected by the use of anti-chimpanzee rabbit serum and the ability of such serum to agglutinate human red blood cells. Since that time, many new data have been obtained regarding this so-called "Ch factor." In a later publication, these will be presented in detail.

In the report referred to above, it was mentioned that chimpanzees were employed because of the fact that they had been reported to be Rh-negative (Wiener and Wade, '45; Mourant and Race, '46). Having available only two chimpanzees, as well as inadequate testing sera and techniques, led me (Butts, '50) to report a confirmation of this statement. Subsequent tests have demonstrated that these two chimpanzees were relatively weak reactors insofar as the Rh or Rh-like factor is concerned.

[1] Assisted by Joann E. Kelly and Vivian M. Dahms of the Medical Research Foundation of Dade County, Florida. We are particularly indebted to Billy G. Mann and David R. Denis of the Anthropoid Ape Research Foundation for putting at our disposal and bleeding 8 of the 17 chimpanzees reported on, and to Mr. Mann also for assisting in the bleeding of the chimpanzees at the Yerkes Laboratories. We are obliged to Drs. K. S. Lashley and H. W. Nissen and other personnel of the Yerkes Laboratories of Primate Biology for allowing us to bleed 7 of their chimpanzees and for assisting us in the process.

No similar blood studies have been made on any of the chimpanzees included in this report. Since the completion of this manuscript, a brief communication by Wiener ('52) has been brought to the attention of the author. It is apparent that the studies on the chimpanzee were carried out simultaneously, as our first tests proving an Rh_0 and hr′ positive chimpanzee were made in July of 1952.

[2] Reviewed in the Veterans Administration and published with the approval of the Chief Medical Director. The statements and conclusions published by the author are the results of his own study and do not necessarily reflect the opinion of the Veterans Administration.

We have since been fortunate to have available for study in the State of Florida a relatively large number of chimpanzees at the Anthropoid Ape Research Foundation, Dania, and the Yerkes Laboratories of Primate Biology, Orange Park, in addition to two chimpanzees now maintained in our own colony at the South Campus of the University of Miami located in Richmond, Florida. From these sources, 17 chimpanzees have been intimately studied insofar as the more common blood agglutinogens are concerned.

Of these animals, 8 were African-born and 9 were born in captivity in this country. Ten were males and 7 females, all varying in age from 7 months to 12 years. Sixteen of the 17 can be classified according to Yerkes ('43) as *Pan troglodytes troglodytes, P.t. verus,* or *P.t. schweinfurthii.* We were extremely fortunate in having available for study the only known pygmy chimpanzee *(Pan paniscus)* in the United States. This animal is the property of the Anthropoid Ape Research Foundation.

MATERIAL AND METHODS

Chimpanzee blood

All chimpanzee bloods were obtained by veni-puncture without any form of anesthesia or sedation. After withdrawal, the blood was placed in tubes containing a dried mixture of potassium and ammonium oxalate, merthiolate and heparin. The tubes were then transported to the laboratory in an iced container as quickly as possible. In the case of bloods obtained from the Yerkes Laboratories, a period of approximately 18 hours elapsed whereas other specimens were delivered within a period of one hour. Studies indicated that the bloods of all chimpanzees were suitable for testing. All bloods were washed three times with sterile saline prior to any of these studies. In all tube agglutination reactions, a 2% saline suspension of such cells was employed with the exception of the tests for blocking antibody in which a 2% suspension of cells was prepared in 20% buffered bovine albumin.

Grouping and typing sera

All sera, except the anti-Rh_0 serum used in the tube test and for absorption, were standard sera obtained from a recognized commercial laboratory.

Anti-A and anti-B sera. Each serum contained a mixture of agglutinating and blocking antibodies and had a protein concentration of 6%.

Anti-M and anti-N sera. These were sera of low protein content. No studies were made to determine whether the antibody was agglutinating or blocking.

Anti-Rh_0 (anti-D) serum. The anti-D serum employed for slide testing with whole blood had a blocking antibody titer of approximately 1–200 and a protein concentration of approximately 28%. The anti-Rh_0 serum employed for tube tests was from a woman immunized against Rh_0 by pregnancy. It contained no alpha antibody. The titer in saline was 1–64 and in 20% albumin 1–128 with human cells.

Anti-rh′ (anti-C) and anti-rh″ (anti-E) sera. These sera were mixtures of agglutinating and blocking antibody (titer 1–64) with a protein concentration of 28%.

Anti-hr′ (anti-c) serum. This consisted entirely of blocking antibody (titer 1–64) with a protein concentration of 28%.

Slide tests. All slide tests were performed by mixing one drop of the respective sera with two drops of whole blood, mixing thoroughly and then rocking the slide on a 45° to 50°C. view box for a maximum period of two minutes.

Tube tests. All tube tests were performed by delivering one drop of serum and one drop of a 2% suspension of washed red blood cells to the bottom of the tube and shaking to mix them thoroughly. The tubes were then placed in a water bath at 37°C. for 30 minutes and then centrifuged at 2000 r.p.m. for two minutes. All agglutination reactions were read by at least two workers.

RESULTS

ABO blood groups

Fourteen (82.3%) of this group were of group A, while three (17.7%) were group O. These figures are in relatively

close agreement with those reported by Wiener ('43) in which a total of 92 chimpanzees had, to that time, been studied, of which 81 (88%) belonged to group A and 11 (12%) to group O.

M-N blood types

Although it has been reported (Landsteiner and Levine, '28; Wiener, '38) that the blood of chimpanzees may contain an N-like agglutinogen, we have not been able to confirm this. All chimpanzee blood studied by us has been strongly agglutinated by anti-M serum, but it is possible that by continued studies on more animals, some of N-type may be found.

Rh and Hr-like factors

Of prime importance in this present study was the testing for the Rh and Hr factors, since both Wiener and Wade ('45) and Butts ('50) had previously reported the chimpanzee to be Rh-negative.

High titer anti-Rh_0 (anti-D), anti-rh′ (anti-C) and anti-rh″ (anti-E) sera were employed for the study of 17 chimpanzee bloods included in this report.

The cells of all chimpanzees reacted with anti-Rh_0 (anti-D) serum when tested by the slide method. The appearance time for agglutination ranged from 10 to 45 seconds. Relatively strong agglutination occurred after two minutes' observation. No reactions were observed with anti-rh′ (anti-C) or anti-rh″ (anti-E) sera.

Slide tests with anti-hr′ (anti-c) were positive for each chimpanzee studied. With this serum, the appearance time ranged from 22 to 65 seconds with relatively weak agglutination after two minutes. These tests support the observation reported by Wiener and Wade ('45) that chimpanzee cells possess an Hr factor.

Tube tests with anti-Rh_0 (anti-D) and anti-rh′ (anti-C) sera confirmed the results of the slide tests. It will be noted (table 1) that the test with anti-rh′ (anti-C) serum was not run on all of the animals.

Thirty per cent bovine albumin was run as a control to prove that the bovine albumin present in the typing sera used was not responsible for the positive agglutination reactions herewith reported. In no case did any agglutination occur when the chimpanzee cells were mixed with 30% albumin.

A positive agglutination reaction with anti-Rh_0 serum, and a negative reaction with anti-rh′ serum and anti-rh″ serum, lead us to the tentative conclusion that the cells of the chimpanzees in our series are all Rh-positive.

ABSORPTION STUDIES

Indirect Coombs' tests and antibody absorption studies were carried out to confirm the conventional Rh studies.

Technique

The same anti-Rh_0 human serum as employed in the test tube agglutination studies was inactivated at 56°C. for 30 minutes and divided into 4 separate and equal volumes. Each portion was then absorbed at 37°C. for 30 minutes by the addition of equal volumes of washed, packed cells. One volume was absorbed with group AM Rh-positive human cells. The second portion was absorbed with OM Rh-positive human cells and the two remaining portions were absorbed with OM Rh-positive and AM Rh-positive chimpanzee cells respectively. The tubes were then centrifuged at 2000 r.p.m. until the cells were thoroughly packed. The supernatant sera were transferred to clean tubes and the residual cells washed 4 times with saline solution for the Coombs' tests. A total of three absorptions was carried out as above described using equal volumes of fresh, washed and packed human and chimpanzee cells.

Coombs' test (slide technique)

The Coombs' test run on the cells from the chimpanzees referred to above were positive following absorption at 37°C. for 30 minutes. In the case of the group A chimpanzee, the appearance time for the reaction was 6 seconds with complete

TABLE 1

NO.	HISTORY			ABO AND M-N REACTIONS			Rh-Hr REACTIONS (Slide tests)						Rh_o and rh′ REACTIONS (Tube tests)		CONTROL (Slide tests)
	Sex	Where born	Age (yrs.)	Group	Anti-M	Anti-N	Anti-Rh_o (anti-D) reactions		Anti-rh′ (anti-C)	Anti-rh″ (anti-E)	Anti-hr′ (Anti-c) reactions		Anti-Rh_o (anti-D)	Anti-rh′ (Anti-C)	30% Bovine albumin
							App. time (sec.)	Comp. time*			App. time (sec.)	Comp. time*			
1	M	Africa	3 ±	A	+	—	30	3 +	—	—	40	2 +	4	—	—
2	M	Africa	4 ±	A	+	—	45	3	—	—	55	2	4 —	—	—
3	M	Africa	9–10	O	+	—	15	2	—	—	22	2	2	—	—
4	M	Africa	10–11	O	+	—	25	3	—	—	35	2	2	—	—
(5)	F	Africa	12	A	+	—	30	3	—	—	40	2	3	—	—
6	M	U.S.A.	4	A	+	—	25	4	—	—	35	2	3 —	—	—
7	F	Africa	10	A	+	—	20	4	—	—	40	2 +	4 —	—	—
8	M	U.S.A.	5	A	+	—	40	2	—	—	60	1	1	—	—
9	F	Africa	3.5	A	+	—	35	3	—	—	45	1	2	—	—
10	M	Africa	6	O	+	—	45	2	—	—	45	1	1	—	—
11	F	U.S.A.	1 ±	A	+	—	45	4	—	—	60	3 +	4 —	NR	—
12	F	U.S.A.	2 ±	A	+	—	10	4	—	—	30	3 +	4 —	NR	—
13	F	U.S.A.	0.5 ±	A	+	—	25	3	—	—	65	1 +	4 —	NR	—
14	M	U.S.A.	2.5	A	+	—	22	4	—	—	35	3 +	4 —	NR	—
15	F	U.S.A.	3 ±	A	+	—	22	4	—	—	35	3	4 —	NR	—
16	M	U.S.A.	3 ±	A	+	—	20	4	—	—	30	4	4 —	NR	—
17	M	U.S.A.	3 ±	A	+	—	25	3	—	—	35	2	4	NR	—

App. — Appearance time.

* Degree of agglutination at end of two minutes.

N.R. — Test not run.

(5) — Pygmy chimpanzee (Pan paniscus).

agglutination at 26 seconds. The group O chimpanzee showed an appearance time of 4 seconds with complete agglutination at 16 seconds.

Agglutinating and blocking antibody titers

Although two human bloods (AM Rh-positive and OM Rh-positive) and the two chimpanzee bloods (AM Rh-positive and OM Rh-positive) were absorbed as described above, the reactions for only one chimpanzee (no. 5, table 1) and a corresponding group human blood are shown in table 2. The reason for selecting chimpanzee no. 5 was twofold. First, the majority of chimpanzees belong to group A. Secondly, it was most interesting to us to study the behavior of the blood of the pygmy chimpanzee as compared to group O chimpanzees of other species.

The original agglutinin antibody titer for human cells of the anti-Rh_0 human serum used in this study was 1–64. Following the first absorption with AM Rh-positive human cells, this titer dropped to 1–2. The second absorption with fresh cells from the same individual removed all anti-Rh_0 antibody. Results following absorption with AM Rh-positive chimpanzee cells were almost identical with the results following absorption with human cells.

High protein titrations run on the same serum showed an initial titer of 1–128 when checked against AM Rh-positive human cells. After the first absorption with AM Rh-positive human cells treated according to the method of Griffitts ('49), the blocking antibody titer was still positive in a titer of 1–32. The second absorption reduced this titer to 1–8. However, this serum was still positive in a dilution of 1–2, after the third absorption. Absorption and testing of this serum with AM Rh-positive chimpanzee cells showed results which differed only slightly from those obtained with human cells. Here, it can be seen by reference to table 2, that the titer prior to absorption with chimpanzee cells was 1–256. Following the first absorption, the titer was reduced to 1–4; the second absorption reduced it to 1–1. The third absorption

TABLE 2

AM Rh^+ human cells

STATUS OF THE ANTI-Rh_0 SERUM	AGGLUTINATING ANTIBODY TITRATION										COOMBS' TEST (Slide technic)		AVIDITY TEST (Slide test)	
	1-1	1-2	1-4	1-8	1-16	1-32	1-64	1-128	1-256	1-512	App. time (sec.)	Comp. time (sec.)	App. time (sec.)	Comp. time*
Before absorption	4	4	4	4 —	4 —	3	1 +	0	0	0			9	4
After 1st absorption	3	2	0	0							Immediate	7	105	1 —
After 2nd absorption	0	0									12	35	0	0
After 3rd absorption	0	0									0	0	0	0
BLOCKING ANTIBODY TITRATION**														
Before absorption	4	4	4	4	4 —	3 +	3 —	2	NR	NR				
After 1st absorption	4	4 —	3 +	2	2	1 +	0							
After 2nd absorption	4	3	2 —	1 —	0									
After 3rd absorption	2	1	±	0										

AM Rh_0 chimpanzee cells

STATUS OF THE ANTI-Rh_0 SERUM	AGGLUTINATING ANTIBODY TITRATION										COOMBS' TEST (Slide technic)		AVIDITY TEST (Slide test)	
	1-1	1-2	1-4	1-8	1-16	1-32	1-64	1-128	1-256	1-512	App. time (sec.)	Comp. time (sec.)	App. time (sec.)	Comp. time*
Before absorption	4	4	4 —	3	3	2	1	0					45	2 +
After 1st absorption	NR	2 +	1	0							6	26	0	0
After 2nd absorption	0	0									0	0	0	0
After 3rd absorption	0	0									0	0	0	0
BLOCKING ANTIBODY TITRATION**														
Before absorption	4	4	4	4 —	4 —	4 —	3	2	1	0				
After 1st absorption	NR	2	1	±	0									
After 2nd absorption	1 +	±	0											
After 3rd absorption	0	0												

App. — Appearance time.
* — Degree of agglutination at end of two minutes.
** — Cells treated prior to absorption with cholera extract as recommended by Griffitts.

completely removed the blocking antibody for chimpanzee cells. Essentially, the results obtained with the other human and chimpanzee blood, which were absorbed and tested in like manner, were the same as those shown in table 2.

SUMMARY

1. Seventeen chimpanzees have been studied, 8 of which were African born and 9 born in captivity.

2. For the first time, to our knowledge, such studies have been made on the pygmy chimpanzee *(Pan paniscus)*. There was no significant difference in the blood of this species from any other species included in our series.

3. Fourteen (82.3%) of the chimpanzees studied by us were group A and three (17.7%) were group O.

In our series, we failed to find the blood of any chimpanzee reacting with anti-N serum. Thus we must assume that this entire group possessed only an M-like agglutinogen.

4. Slide tests with high titer anti-Rh_0 (anti-D), anti-rh′ (anti-C), anti-rh″ (anti-E) and anti-hr′ (anti-c) showed all chimpanzees in our studies to be Rh_0 hr′ positive. Tube tests with anti-Rh_0 (anti-D) and anti-rh′ (anti-C) sera confirmed the slide tests. The control slide agglutination tests using a 30% bovine albumin failed to agglutinate the cells from any of the chimpanzees included in this report.

5. Coombs' tests run on absorbed group O and group A chimpanzee cells were positive.

6. Agglutination tests run with saline dilutions and protein dilutions of serum from a woman immunized against Rh_0 by pregnancy showed marked agglutination of both group A and group O humans and chimpanzees prior to absorption. The agglutinin was completely removed from this serum after the second absorption with both human and chimpanzee cells. The blocking antibody was still present in a 1–2 dilution after the third absorption with human cells when tested against AM Rh-positive human cells. However, tests with AM Rh_0 chimpanzee cells after the third absorption with chimpanzee cells were negative.

7. Blood agglutination and absorption studies made on 17 chimpanzees show that in every case the Rh_o factor is present. Thus the blood of all chimpanzees of this series is Rh-positive.

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VIKING FUND MEDALIST FOR 1952

The American Association of Physical Anthropologists has selected for the 1952 Viking Fund Medal and Award, its president, Dr. William Louis Straus, Jr. The Awards Committee of the Association was unanimous in its choice.

WILLIAM LOUIS STRAUS, JR.

Doctor Straus was born, and has spent most of his life, in Baltimore. Except for one year of undergraduate study at Harvard he received both his college and graduate training at the Johns Hopkins University. While still an undergraduate he read avidly the standard anthropology texts. He was particularly fascinated by Keith's "Antiquity of Man," Osborn's "Men of the Old Stone Age" and Sollas' "Ancient Hunters," and so he had an early interest in the origin and antiquity of man.

As a graduate student in anatomy his research on "The growth of the human foot and its evolutionary significance" was directed by Dr. Adolph Schultz. Then came the realization that he wanted to learn a great deal about living primates as well as the gross, histological, and neurological aspects of human anatomy. Dr. W. K. Gregory, among others, was very kind to him and greatly encouraged his interest in primates; he has remained his good and encouraging friend even though through the years their views on human and primate evolution have become somewhat divergent.

After receiving his doctorate in 1926 Doctor Straus spent a year at Western Reserve University as a National Research Council Fellow. He worked in the Department of Anatomy with Professor T. Wingate Todd studying the comparative anatomy of the pelvis and the racial and sexual characters of the human pelvis. He returned to Hopkins as instructor in anatomy and to his association with Doctor Schultz. This happy association continued with only one interruption until 1950 when Doctor Schultz returned to Switzerland. For the first 10 years of this period he came "under the spell" also of other anatomists in the department — Ernst Huber, Brazier Howell, and George Wislocki, all working in comparative anatomy; Marion Hines in neurology — and of Carl Hartman in the Department of Embryology of the nearby Carnegie Institution. At intervals he was attracted to special dissections of some of Schultz's rare specimens before their skeletonization.

In 1937–38 Doctor Straus was in England as a Guggenheim Fellow working in the Departments of Anatomy at University College, London, with Professor H. H. Woollard and at Cambridge University with Dr. D. H. Barron, on the subject of the activity of striated muscle.

Back again at Hopkins his interest became more concentrated on primates, particularly on the morphology of hands, feet, and muscles of the extremities. At the same time he developed an interest in the history of science through his contacts with the medical historians, particularly Dr. Oswei Tempkin. They have published two papers jointly, one on Vesalius and one on Galen. The latter deals with Galen's description of the muscles of the arm in the Barbary ape.

Very lately, Doctor Straus has turned his attention to human fossil remains. His interest in these remains stems, of course, from his ideas on the evolution of locomotion and posture.

Until 1952 when Doctor Straus became professor of physical anthropology at Hopkins all his appointments had been in human anatomy. Dr. T. Dale Stewart has said, "He has a superb knowledge of gross and microscopic human anatomy — all too rare today — which, together with a wide knowledge of comparative anatomy, he has brought to bear on problems of human evolution." His experience extends to many animal forms: paramecia, urodeles, lizards, ungulates, edentates, cats, rats, pigs, whales, monkeys, anthropoids, and humans. At present he has a paper in press (with Mary Rawles) concerning development of chick tissues in coelomic grafts. His list of publications, heavily weighted with morphological studies of the muscular, skeletal, and nervous systems, includes also studies on viscera, nerve physiology, and histology of the skin. Doctor Schultz has written me from Zürich that, "Doctor Straus' outstanding many-sidedness is due to his unusual talent for absorbing what goes on around him. His work is a symbol and a shining example of the close relation between anatomy, comparative anatomy, and physical anthropology and of the value of the former sciences for the latter."

This varied program has enabled Doctor Straus to formulate important evolutionary concepts or to deny them. Concerning the principle of true nerve-muscle specificity he believes that there is no evidence of the existence of a specific, inherent attraction between a given muscle fiber and a given nerve fiber but rather any close resemblances in innervation pattern in different species must merely reflect general similarity in development. Because of this, innervation is of great aid in homologizing the muscles of animals belonging to one vertebrate class, but not in homologizing the muscles of animals of different classes.

Another concept, important especially to physical anthropology, has resulted from his weighing the data supporting the anthropoid and non-anthropoid theories of human origin. He has presented further evidence that numerous characters in man — both living and fossil — appear to be more generalized or primitive than in the anthropoids. It is his conclusion that a non-anthropoid concept of hominid ancestry is in closer agreement with known facts than is the anthropoid theory. This conclusion was arrived at not only upon comparative-anatomical grounds but also from consideration of paleontological evidence. Thus his studies have contributed effectively to the point of view that man evolved from a terrestrial primate who in turn evolved from a quadrupedal arboreal form rather than from a brachiating form. Doctor Straus maintains, that "this concept, ...

is naturally no more than a working hypothesis the final evaluation of which must be left to the future. For the problem of man's ancestry is still a decidedly open one, a riddle."

Speaking for the American Association of Physical Anthropologists I am happy, Doctor Wenner-Gren, to present Dr. William Louis Straus, Jr., for the Viking Fund Medal and Award for 1952, in recognition of "his outstanding work in the general field of man's (evolutionary) relationship to subhuman primates."

MILDRED TROTTER
Vice-President

BIOPHYSICAL RESEARCH METHODS. Edited by Fred M. Uber. Interscience Publishers, New York. ix + 667 pp. 1950. $9.50.— The title of this book would not in itself attract many physical anthropologists, even though our investigative techniques are primarily biophysical in nature. However, a number of chapters cover techniques of considerable importance, some of which are being used, and others which will be used in anthropological studies. Graduate students in particular need to know more about x-ray techniques, radioisotope studies, and thermometry than we do.

The first chapter should be of special interest. Titled "avoid fruitless experiments" and written by the editor, it is a concise how, what and why not of experimentation. It includes also a rather hard-headed discussion on publication. In fact with one exception chapter 1 might be assigned to all graduate students. And that exception is titled "choose a genetically constant organism"! Sound advice, but our organism of choice is man.— S. M. Garn.

BRIEF COMMUNICATIONS

FLUORINE TESTS RELATIVE TO THE KEILOR SKULL

EDMUND D. GILL
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ONE FIGURE

Where Dry Creek debouches into the Maribyrnong River near Keilor, Victoria, Australia, is a quarry for molding sand from which, in 1940, a human skull was collected. Keble and Macpherson ('46, p. 52) found reason for believing that the skull might have been a burial, so the writer applied the fluorine test in an effort to determine whether or not its age is that of the Keilor Terrace in which it was found. The Chief Chemist of the State Laboratories of Victoria, Mr. W. R. Jewell, and his staff kindly carried out the requisite analyses, the results of which are listed in table 1. Fossils are very rare in the Keilor Terrace, and those shown in table 1 are all that have been found, in spite of constant search. The fluorine percentages are rounded off to the nearest 0.05, this being considered near the limit of significant figures. The two samples of *Rattus* were different groups of bones of the same specimen. The fluorine index for this animal is high, and one wonders if it is due to rats ingesting the bones of other animals, thus presumably gaining extra fluorine. However, the results of the fluorine test indicate that the human skull was *in situ*, and not a recent intrusive burial. Its type of preservation is in keeping with this. Also, the position of the skull in the terrace was such that, if it were a burial, an excavation of either 9 feet from the top of the terrace, or 25 feet from the bank of Dry Creek, would have been necessary — too far for an aboriginal burial (fig. 1). Moreover, the quartzite flake (Mahony, '43b) and layer of burnt bone, ash, and red ochre (Keble, '46; Keble and Macpherson, '46) provide evidence of human occupation at the time it was laid down.

Although the Keilor skull is of the age of the terrace in which it was found, that age is not as great as originally postulated (Mahony, '43a, b; Keble and Macpherson, '46). The Braybrook Terrace is but

an eroded part of the Keilor Terrace, for it has the same lithology, the same internal structures (including the diastem shown in fig. 1), and the same soil. There is a terrace older than the Keilor Terrace. The three depositional terraces now recognized can be differentiated by their lithology, internal structures, soils, and spatial relationships in the valley. In the writer's opinion, the Keilor Floodplain has nothing to do with eustatic changes of sea-level, but is a function of restriction by the narrow winding gorge at the downstream end plus changing climactic conditions. It has been discovered that a marine transgression intruded at least 11 miles up the lower end of the

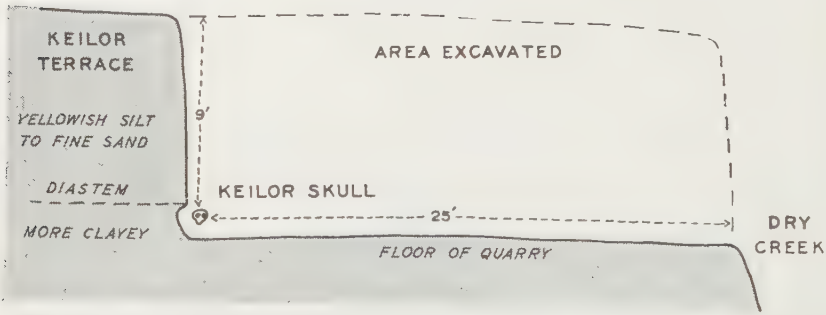

Fig. 1 Section showing Keilor Terrace and approximate situation of the Keilor skull. Also shown are distances which would be involved if the skull had been an intrusive burial.

TABLE 1

Fluorine/phosphate ratios for the Keilor skull and other fossils from the same site

SPECIMEN	% F	% P_2O_5	$\frac{\% F \times 100}{\% P_2O_5}$	NUMBER OF DETERMINATIONS
1. Keilor skull (inside of right petrous temporal)	0.30	14.9	2.0	1
2. Keilor skull (outside of right squamous temporal)	0.30	15.3	2.0	1
3. *Macropus* sp. vertebra	0.35	18.8	1.9	1
4. *Vombatus* sp. humerus	0.40	26.7	1.5	1
5. Bone fragment	0.85	29.7	2.9	1
6. *Rattus* sp.				
sample *a*	0.75	19.6	3.8	1
sample *b*	0.50	11.3	4.4	2

Maribyrnong River valley, and the resultant fossiliferous formation interdigitates with the terraces. The marine formation is being dated by radiocarbon, and it is hoped thus to get at the age of the Keilor skull. No substance suitable for radiocarbon analysis has been found by the writer in the Keilor Terrace.

The Chief Commissioner of Victorian Police, Mr. A. M. Duncan, has kindly investigated matters relative to Mahony's mention of a second human skull from Keilor (Mahony, '43b, p. 31), and to make a long story short, it transpires that there was no second skull.

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Note. Detailed information concerning the fluorine tests on the Keilor skull and bones from other sites in Victoria will appear in Memoir 19 of the National Museum of Victoria, Melbourne, due to be published later this year.

THE FOURTH INTERNATIONAL CONGRESS OF ANTHROPOLOGICAL AND ETHNOLOGICAL SCIENCES, 1952

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The session held in Vienna, September 1–8, 1952, was the second post-war meeting of the International Congress of Anthropological and Ethnological Sciences. The previous session was held in Brussels in 1948; the two earlier Congresses, in 1934 and 1938, met in London and in Copenhagen respectively. (The Permanent Council announced that the 5th meeting will be in Philadelphia.)

The roster of the 4th Congress lists 694 full members, 142 associate members (most of them wives of members) and 20 institutional memberships. Of the 39 full members from the United States, 5 are

[1] Delegate, The American Association of Physical Anthropologists and the American Association of Anatomists.

included in the current membership of the American Association of Physical Anthropologists. As would be expected, Austria and some of the nearby countries are well represented. The full members from these countries number, approximately: Austria, 175; Germany, 120; England, 50; France, 45; Italy, 40; Belgium, 30; Netherlands, 20; Switzerland, 20. Almost every other nation is represented, each with from one to several members. These figures, it should be emphasized, are drawn from the printed membership list rather than from actual attendance. In this as in other international congresses there were many members, and even a few who had been scheduled to present papers, who did not attend.

The Congress was opened with an address by the President of the Austrian Republic, Dr. Theodor Körner. Other general sessions of the Congress, held mostly at night, were devoted to a wide range of topics; one session concerned the relation of UNESCO to anthropology and the UNESCO statement on race.

The scientific program lists over 400 items. The diversity of interests featured in the Congress is reflected in the designations of sectional meetings: history and methods of ethnology, sociology; religions; art, music and the dance; cultivated plants and domesticated animals; schools and ethnology; Europe; North Africa and Southwestern Asia; Africa; India; Far East; Australia and Oceania; America; prehistoric archeology and paleo-ethnology; demography; psychology; linguistics. Papers in physical anthropology, 118 in all, were scheduled in 4 sections that ran concurrently: general anthropology (22 papers); special anthropology (30), paleo-anthropology (22), special anthropology (23), biological anthropology (38). The three sectional programs exclusive of paleo-anthropology comprise a wide variety of studies. Well over half of the papers concern phases of relatively recent emphasis, notably genetics, constitution, blood groups and sickling.

On one of the afternoons, the Institute of Anthropology of the University of Vienna was visited by interested members for a guided tour and for viewing exhibits of work in progress; the Director (J. Weninger) presented a communication on the research program of the Institute.

Among the social events were: an informal gathering on the night before the opening of the Congress, a reception by the Lord Mayor of Vienna, a reception by the Federal Chancellor of Austria, and an evening of folk music and dancing. Additional entertainment, including sightseeing and shopping trips, was provided for the wives in attendance.

The organization committee, under the presidency of P. Wilhelm Schmidt, had prepared ably for smooth conduct of the whole Congress.

SPECULATION ON THE SIGNIFICANCE OF MUSCLE-BONE RELATIONSHIP IN TERMS OF HUMAN EVOLUTION

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ONE FIGURE

The ultimate aim of human paleontology has been to extrapolate from the fragmentary osseous remains of man's ancestors a complete and functional understanding of the animals. Washburn ('50) has pointed out the need for extreme care and a sound knowledge of the intimate relationships between bones or portions of bones and the soft tissues which clothe them before this reasonably can be accomplished. This brief communication has as its purpose to point out another area where our information is deficient and to appeal for research designed further to elucidate the general problem of muscle-bone relationships in our conceptual scheme of man's evolution.

I reproduce herewith data (fig. 1) from "The effect of growth and development on the composition of mammals" by Christine M. Spray and Elsie M. Widdowson which appeared in the British Journal of Nutrition ('51). This collection of biochemical data in a technical report probably has been seen by few if any physical anthropologists. The figure has been redrawn to emphasize certain of the data and brackets have been added, but the values have not been changed. It should be stressed that this work, performed at the Department of Experimental Medicine, University of Cambridge, represented the modern and complete techniques available to modern biochemistry.

Figure 1 presents the results of total carcass analyses on 5 mammals including man. The data given are mean values for a large number of laboratory animals and the few available human adults. In order to invest the purely chemical results with their appropriate meaning in terms of gross morphology, I have made two chemical linkages: protein and potassium as indicative of muscle tissue; and sodium, calcium, and phosphorus as representing bone. In justification for this arrangement of the data, it is realized that all the body protein is not present as muscle tissue, although it constitutes a majority. Roughly 75% of the potassium is in the muscles, and the potassium and protein values are basically similar. Bone is easier to equate with certain of the chemical elements represented in figure 1. Approxi-

mately 99% of the calcium and 90% of the phosphorus in the body are concentrated in bony tissue, and although only about 25% of the body sodium is non-exchangeable bone sodium, the sodium values are clearly influenced by this fraction (Shohl, '39).

The significance of the values shown in figure 1 can be summarized into two points. (1) The muscle-bone relationship in man is clearly and markedly different than found in the other animals. (2) Man is not aberrant in the amount of muscle tissue per 100 gm of fat-free tissue, but he is unique in the great concentration of bone. The calcium and phosphorus values are almost double that found in the other animals, and the sodium value is approximately 50% higher. This discrepancy

		RAT	RABBIT	CAT	PIG	MAN
	WEIGHT (kg)	0 35	2.6	4.0	125	65
MUSCLE	*PROTEIN (g.)*	*22.1*	*23 2*	*21 0*	*19.6*	*19.4*
MUSCLE	WATER (g)	73 7	72 8	74 4	75.6	72.8
MUSCLE	SODIUM (mg.)	150	150	150	150	217
MUSCLE	*POTASSIUM (mg.)*	*300*	*300*	*300*	*280*	*280*
BONE	CALCIUM (mg.)	1300	1300	1300	1200	2305
BONE	MAGNESIUM (mg)	40.0	50 0	45.0	45.0	45.5
BONE	PHOSPHORUS (mg.)	700	700	800	700	1345
	IRON (mg)	6 0	6 0	6.0	9.0	7.4
	COPPER (mg)	0 2	0 15	0 15	0.25	0.17
	ZINC (mg.)	3.0	5.0	2.3	2.5	2.8

Fig. 1 Comparison of the chemical composition of adult animals, including man. (All results expressed per 100 gm of fat-free tissue.)

is so great and the other results so consistent that it would be impossible to ascribe man's bone-muscle relationship to experimental error.

I have tried to transpose the chemical data into morphological entities. What is the biological speculation as to the significance of these facts? During a recent visit to this country, R. A. McCance, head of the Cambridge department where these experiments were carried out, made two suggestions about this relationship. The first was that the apparently disproportional presence of bone in modern man must be related to the requirements of upright posture and bipedal gait. His second comment is less likely to occur to an anthropologist but is equally stimulating. He observed that the large concentration of inorganic salts found in the fat-free tissue of man could not accumulate in an animal who lacked a prolonged growth period. Both upright posture and delayed maturation are important in the

evolution of modern man, and it would be fruitless to speculate on cause and effect without further evidence.

It would be possible to gain indirect evidence regarding the unique position of man in bone-muscle relationship by comparable analyses of modern primates. Anthropoids may be prohibitively expensive to sacrifice in this manner, but there must be several species of monkeys whose monetary value is distinctly less than that of an adult pig. Bone and muscle ratios similar to man in the lower primates would certainly establish this as an old primate characteristic, and its further elucidation would then depend on the interest and ingenuity of primatologists. If the reverse were found to be the case, some sampling in the higher primates would be indicated to bracket the relationship in our scheme of evolution.

If we assume that a large quantity of bone in relation to a given mass of tissue by weight is a peculiarly human characteristic, we raise problems in the interpretation of modern man's ancestry. We are all familiar with the pre-human fossils, usually placed somewhere in the phylogeny of man, which are characterized by massive osseous remains. If these remains are accepted as the precursors of modern man, we must postulate a still greater discrepancy from the mammalian pattern of bone versus muscle or clothe these bony remains with fantastic quantities of muscle. There must be limits to the former explanation because an even more marked imbalance may eventually result in an animal with poor propulsive qualities on land. For that matter, what must we deduce about the length of the maturation period in fossils characterized by such massive bony remains?

We all repeat and perhaps even believe the statement that modern man has undergone a loss of muscle tissue in his past history. The comparison on muscular attachment areas on modern and fossil man suggests this process. Perhaps he has lost some superficial bone, but how can we postulate the loss of much bony mass in light of the values given by Spray and Widdowson? We can hope to reach a reasonable picture of man's ancestry only by the successful integration of diverse bits of evidence from various sources, and I submit that a new and suggestive line of inquiry has turned up in a surprising area of investigation. Its further pursuance and integration will be largely up to our profession.

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WASHBURN, S. L. 1950 The analysis of primate evolution with particular reference to the origin of man. Cold Spring Harbor Symposia on Quantitative Biology, *15:* 67–78.

THE HAIR AND SCALP. A Clinical Study (with a chapter on hirsuties). By Agnes Savill. Edward Arnold and Company, London. xi + 316 pp., 58 figs. 4th ed. 1952. $5.50.— Savill's book, though less well known in this country, has been a classic in England and the commonwealth nations since the publication of the first edition in 1935. This 4th edition is noteworthy for the many photomicrographs, a chapter by Astbury on the molecular structure of the hair, and sections on hair dyes, dandruff, etc. "The Hair and the Scalp" is not a comparative study; it does not overlap with Danforth, and it is primarily directed at the clinician. Nevertheless the description of the various pathological conditions that affect the hair and scalp, a good but short section on the theory of the "permanent" wave, and like features commend it to the attention of the physical anthropologist interested in the ectoderm and its derivatives.— S. M. Garn.

THE ANTHROPOLOGY OF IRAQ. Henry Field. (Nos. 2–3. Kurdistan and Conclusions. ix + 176 pp., 9 charts, 187 tables, 29 graphs, 76 collotype figures. Papers of the Peabody Museum, Vol. XLVI, Peabody Museum, Cambridge, 1952).— This report, together with the two preceding it, complete the presentation of data gathered at different times since 1925 on the anthropology of Iraq. The material bearing on the physical characteristics of the inhabitants is voluminous and traditional descriptive anthropometry. Being from work done by different people at different times, strict comparability is lacking and unevenness characterizes the report. As one conclusion, Field states that "when the ancient skeletal material is examined, we find that the basic population of Mesopotamia has remained unchanged for at least six millennia."

Whether this monumental accumulation of data will be useful for comparative studies or for others whose problems are beyond the descriptive level will remain to be seen, yet there is little doubt that as an anthropological account of one people this series is unique. — F. P. Thieme.

REVIEWS

LES HOMMES FOSSILES. ÉLÉMENTS DE PALÉONTOLOGIE HUMAINE. By M. Boule and H. V. Vallois. 4th edition. Masson et Cie., Paris, 1952. Paper: 3800 fr., cloth: 4400 fr.

Thirty years after the initial edition of Marcellin Boule's *Les Hommes Fossiles,* a 4th edition has appeared, revised and enlarged by Prof. H. V. Vallois. Brought up to date with regard to the newest discoveries of fossil men, and with an additional 5 text figures, the text is still 5 pages shorter than the third edition revised by Professor Vallois in 1946. As before, the book is lucidly written and admirably illustrated with charts, drawings and photographs. The original format has been little altered from the earlier editions. There are chapters on early work in prehistory, chronology, and a brief section on Tertiary and living primates. Other sections deal with the Asian "prehominids," lower Pleistocene forms of Europe (pre-Neanderthals and pre-sapiens forms), and "classic" Neanderthals, and the men of the European Upper Paleolithic and "Mesolithic." Separate chapters discuss the evidence from Asia, Africa, and America. No attempt is made here to discuss contents other than the additions and alterations in the new edition.

In the past few years, important advances have been made in knowledge of (1) the South African man-apes, (2) Villafranchian man, (3) the origin of modern forms of man, (4) tool preparation traditions of Africa and Asia. These developments, along with special methods for providing an improved relative and absolute chronology (fluorine and C^{14}), have provided a fresh impetus to postwar prehistoric research. Since these are specific topics noted by Professor Vallois in his preface, they will be briefly discussed here.

The South African man-apes are still included within the chapter on fossil primates and less attention is devoted to the valuable evidence afforded by their postcranial skeletons than that from their skulls. Brief notice is taken of the new discoveries in the Transvaal but the discussion of the group still covers only 7 pages (whereas the fragmentary Piltdown remains are granted 17 pages!). In light of the redating of Piltdown, and the many specimens now known of the man-apes, this hardly seems justifiable on grounds of numbers or phylogenetic importance. The man-apes are regarded as cousins of man because they lived too late, a conclusion as yet unsubstantiated

by accurate dating (except perhaps *P. robustus*). The best evidence for Villafranchian man is provided by evidences of early pebble tools from northwest Africa, East Africa, and the Transvaal, and these are briefly mentioned.

Changes in dating are reflected in the summary chart of Pleistocene events (p. 46–47) which omits the Piltdown remains from their former prior position, places Pithecanthropus at the base of the Pleistocene, and incorporates a series of fossils as "pre-sapiens" and "pre-Neanderthal" at the Riss, Riss-Würm level. No revisions have been effected, however, in the cultural sequence which is reminiscent of the stages established many years ago (although the newest work is considered throughout the text). Such a revision seems necessary, with less attention to western Europe as a key sequence, in light of the recent reanalyses of French mid-Paleolithic assemblages by F. Bordes, the ever-increasing data from central and eastern Europe, and the greatly increased knowledge of prehistory in Asia and Africa. Although the Mindel glaciation is now regarded as Pleistocene (in the third edition as late Pliocene), the Günz phase is still retained in the Pliocene and no mention is made of the pre-Günz or Donau phases of the Alpine sequence. In light of the vast amount of recent data from geomorphic studies on both the continental and marine Pleistocene sequence, a revision of this chart and the chapter on Pleistocene chronology seems warranted. Much material, both cultural and biological, is now at hand for the prehistorian, providing a better picture of past human livelihood and environments than was ever possible to reconstruct before.

Several modifications have been made in the chapter dealing with mid-Pleistocene man. The fossils from Ehringsdorf, Steinheim, and Saccopastore are now discussed as "pre-Neanderthals," a group apparently ancestral to the later "classic" Neanderthals of western Europe. A pre-sapiens group, composed of Piltdown, Swanscombe, Fontéchevade (and perhaps the Quinzano occipital bone from Italy) is regarded as a parallel-evolving phylum leading to modern men. The new fluorine dating of Piltdown is mentioned but there is lacking a much-deserved extended discussion of the significance of these results for human phylogeny. The Smith-Woodward reconstruction of Piltdown is depicted rather than the final, apparently more accurate (if such is possible!) one by Sir Arthur Keith. The Fontéchevade specimens, especially relevant for the parallel-phyla theory, are briefly mentioned as assuring the case for early modern man (contemporaneous with pre-Neanderthals), but no illustration of the quite critical glabellar fragment (no. 1) is figured. In another section, the Mount Carmel fossils are regarded as "a variety of very evolved Neanderthal man."

Excellent chapters on the Upper Pleistocene and "Mesolithic" fossils summarize the great amount of scattered data from this time period. Three European Upper Paleolithic groups are still recognized — Grimaldi (the oldest and "certainly Africans"), the Aurignacian Cromagnons from Asia (with several varieties including Predmost- Combe Capelle-Obercassel and Mechta), and the Magdalenian Chancelade group (of more northerly derivation). Four main "Mesolithic" types are also defined (based on the cranial index): (1) a brachycranic Ofnet group, (2) a disharmonic dolichocranic Ofnet group (like Nordics), (3) a disharmonic, mesocranic Teviec group, and (4) a harmonic, dolichocranic Mugem group (Mediterranean).

Les Hommes Fossiles is a standard text in prehistory and one of the most valuable reference works for those desiring evidence of man's past. It is to be hoped that in future editions, an integration of modern genetic and evolutionary theory be made, both with respect to prehistoric problems and those of modern race formation and systematics. Also that a chronological coverage be made of the Old World (as has been done in the case of western Europe) rather than treating the African and Asian material in separate sections. The broad coverage of this type of work almost demands the cooperation of several workers in diverse specialized fields. Certainly Professor Vallois is to be congratulated for his excellent up-to-date synthesis of the human paleontological and prehistoric data, the above criticisms notwithstanding.

F. Clark Howell
Department of Anthropology
University of Chicago

ELEMENTARY MEDICAL STATISTICS, THE PRINCIPLES OF QUANTITATIVE MEDICINE. By Donald Mainland. ix + 327 pp. W. B. Saunders, 1952. $5.00.

This is a textbook for courses in elementary statistics for medical students. It is also intended for use by investigators in the medical sciences, and they will find it of real value, not so much because of a chapter dealing with the special statistics they may require, as because of the emphasis on the meanings of statistical findings in their field.

The scope of this work is strictly circumscribed. Recognizing the need for use of special methods in some investigations, the author refers the student to other works and advises him to seek personal help when necessary. One can appreciate the comment that the economist, the public health statistician and the mathematician — even if

he specializes in statistics — are accustomed to dealing with data rather different in character from those that occur most frequently in medicine; and that the medical research worker in search of a suitable statistical method is more likely to get it from workers in applied science, in particular agriculture. One wishes it were possible to add "and from physical anthropologists," for the statistical problems faced by the latter are frequently parallel to those of medical research. Both must use simple and yet rigorous methods to arrive at probabilities, for example. Those anthropologists who teach medical students or who are consulted by physicians on problem design or analysis will profit from knowing this book.

The greater part of the work deals with methods of evaluating the significance of statistical data. Nevertheless, there is constant emphasis on the possible gaps between statistical significance and diagnostic or therapeutic meaningfulness. This is illustrated by numerous examples from the medical literature which the student is challenged to interpret for himself before referring to the author's analyses. For instance, the author lists a series of questions concerning the whos, whys, whats and wherefores of investigation. When the student has been directed how to think about evidence, the author shifts to teaching a few techniques of statistical evaluation. Stress is laid on estimation of significance at the 1% and 5% levels; and tables and charts of binomial confidence limits, chi square and t scores are given for various sample sizes at these two levels. Despite a disclaimer in a brief paragraph on "Levels of Significance," the fact that several of the examples have been so chosen as to fall barely within or just outside the 95% or 99% band, may give the student too arbitrary a view of significance. Especially where multiple tests on similar data or on related traits are used, overall significance may require estimation, and the actual levels of probability become more important than the relation to the 95% cut-off point. This seeming arbitrariness is manifest in the author's assertion that "A second test of the same hypothesis with the same data is not permissible." Of course, several tests of the same data are permissible if they are equally applicable, with the reservation that the probability depends on all possible groupings and not alone on that which yields the lowest probability of being a random result.

An excellent feature of this work is the repeated emphasis that, to be able to state one's results in terms of probability, one must start with random samples. Allocation of experimental subjects by use of tables of random numbers is described. (Perhaps it is going a bit too far, however, when the author suggests that values at the center of a scale interval be allocated to the mark above or below at random;

the more usual procedure of consistent allocation to the nearest even — or odd — mark seems adequate.)

The book is arranged in a series of chapters graded in complexity. Each chapter contains numerous practical illustrations from medical studies — frequently manifesting imperfections in design to which attention is called — and each chapter ends with a further series of examples in the form of questions which are answered only at the end of the book. These give practice in interpretation as well as in the working out of problems. A minimum of unnecessary derivation of formulae is included. Cross-references are frequent and will be useful to those who have used the work as a text and wish to apply its lessons. (These references sometimes omit to give page numbers, an unfortunate practice that seems universal in books on statistics, and that adds to the difficulty of using the book for casual study by oneself.)

This is, then, a textbook, unique for its avowed purpose, and a model for similar works introducing statistical methods to other branches of science. In an (apparently unsuccessful) attempt to keep the price down the publishers have produced the book by photo-offset from typescript. Despite this, legibility is adequate and my copy will be in use long after the plastic-treated cardboard cover is gone.

Gabriel W. Lasker
Wayne University
College of Medicine

Comparison of Human and Chimpanzee Development.— A comprehensive explanation of human development must account for the observations which led originally to the application of the theory of recapitulation to early behavioral manifestations, and for such new observations as would conform to this concept. The more obvious chimpanzeelike postures which are seen temporarily during the first year of life in the human infant are (a) those involving the outward rotation and flexed position of the legs while prone or supine,

which Ames refers to a still lower vertebrate in her descriptive phrase, "Legs flex, frog, . . ."; (b) those which call for quadrupedal stance and locomotion; (c) the sitting posture with hands placed for support; (d) the wide separation of the feet in upright standing; and (e) toe flexion in the standing position. Certain items which indicate a predominance of limb flexion and hand closure show a high frequency for human infants early in the first year with subsequent decrease, whereas in the chimpanzee the frequencies either remain high or show an increase. . . . Whereas the human infant outgrows the behavior indicated by all of these items at an early age, the chimpanzee carries them well into the years of childhood or even into maturity. About 30 additional items, some of them similar to the above, can be fitted into the general pattern or are at least not inconsistent with it. The appearance of such "recapitulative" items in early human development is undoubtedly an extremely important manifestation for theoretical genetic psychology. That such items cannot be handled by the old recapitulation theory is obvious. Human and chimpanzee postural development do not conform by running a strictly parallel course until a specific stage, which could be said to mark the cleavage in the course of phylogenesis. Some differences appear early and some similarities are evident at late stages, the lack of parallelism in the sequence having been shown clearly by our data on general body postures. Just as in the case of other so-called theories which we have briefly examined above, the concept of recapitulation in its strict sense does not agree with all of the facts. Like the "principles" of rigid sequential development, the assumption of cortical control, cephalo-caudal development, and so on, the idea of recapitulation can be useful as a descriptive classification of certain observations. When concepts such as these are recognized as useful descriptive categories rather than being proposed as comprehensive theories, the stigma of limited applicability will no longer threaten to force these concepts into complete disrepute.— A. H. Riesen and Elaine F. Kinder. The Postural Development of Infant Chimpanzees. Yale University Press, New Haven. 1952. pp. 181–182.

PROCEEDINGS
OF THE TWENTY-SECOND ANNUAL MEETING
OF
THE AMERICAN ASSOCIATION OF PHYSICAL ANTHROPOLOGISTS

The twenty-second annual meeting of the Association was held on Saturday, Sunday, and Monday, December 27, 28, and 29, 1952, at the University Museum of the University of Pennsylvania, in conjunction with the American Anthropological Association whose meetings extended from December 28 to 30. Ninety-four people attended the AAPA meetings, including 59 members.

The annual dinner was attended by 70 people and held at 7:00 P.M. in the Pennsylvania Room of the Hotel Penn-Sheraton, which served as headquarters for most of the membership. After dinner Dr. Sherwood L. Washburn, retiring as president of the Association, spoke to the title "Our Association," balancing the achievements and possibilities of physical anthropology as related to the variety of abilities contained within the membership. This was followed by the annual Business Meeting and a smoker.

On Sunday morning the American Anthropological Association sponsored a Symposium on Human Nature. Physical anthropology was represented by Dr. S. L. Washburn speaking on "Evolution and human nature" with Dr. Loren C. Eiseley as discussant. On Sunday afternoon, with the assistance of Dr. S. L. Washburn as Moderator, Dr. Josef Brozek led a panel discussion which he had organized on "Measuring nutriture." This was followed by a demonstration of a recently perfected technique for measuring the human body on 4 simultaneously projected full-size images of the standing subject. This is adaptable for photography as well as direct

measurement. The exhibit was staged by Mr. R. S. Bunge of the PhotoMetric Corporation, 51 Madison Avenue, New York City 10, N. Y. After the Business Meeting of the AAA, the University Museum (represented by its director, Dr. Froelich Rainey, assistant director, Dr. Alfred Kidder, Jr., and staff members) welcomed members of both the American Anthropological Association and the American Association of Physical Anthropologists at a cocktail party given from 6–7 P.M. in the Chinese hall of the University Museum.

Monday morning's program featured a symposium on "Methods of determining significant degrees of relationship," organized by Dr. William S. Laughlin and sponsored jointly by the AAA and AAPA.

BUSINESS MEETING, DECEMBER 27, 1952

The President of the Association, Dr. S. L. Washburn, announced that Dr. William L. Straus, Jr., had been selected by the Association as its nominee for winner of the Viking Fund Medal and Award in physical anthropology, to be presented by the Wenner-Gren Foundation at its annual Award dinner on March 6, 1953. The Nominating Committee for 1953 was announced as including Dr. S. L. Washburn (Chairman), Dr. Earnest A. Hooton, and Dr. Bertram Kraus. Doctor Washburn also named Dr. W. L. Straus, Jr. (Chairman), Dr. Carleton S. Coon, and Dr. Mildred Trotter as members of the 1953 Viking Fund Award Committee, thereby including two previous winners and a third referee.

The minutes of the twenty-first meeting of the Association were voted approved as recorded in the Proceedings published in the June, 1952, issue of the American Journal of Physical Anthropology.

The Secretary pointed to the accelerating growth of the Association (1930, 109 members; 1942, 153 members; 1950, 219 members; 1952, 300 members) and announced the Executive Committee's proposal of 15 candidates for membership, who were elected unanimously:

John Chidaine
William S. Cornwell
Nils-Gustav Gejvall
Henry Guze
C. Nash Herndon
Carl-Herman Hjortsjö
George R. Holcomb
John M. Longyear, III
William J. Mayer-Oakes
Harry C. Meyers, Jr.
Carl Michael Seipel
Samuel Selby
Mortimer Spiegelman
William L. Thomas
F. A. Vandervael

The Executive Committee proposed the following revision of Article V of the By-Laws of the Association in order to simplify action by allowing the Executive Committee wider discretion in approval of new members:

Section 1. Membership is open to professional anthropologists, professionals in cognate sciences, advanced graduate students showing evidence of professional capacity, and others who have demonstrated their interest by publication or professional activities.

Section 2. Candidates for membership, duly proposed by two members, shall be considered by the Executive Committee, acting in behalf of the Association; and those approved for membership shall be notified as soon as practical. The actions of the Executive Committee must be ratified by the membership at the next Annual Meeting. Candidates may also be approved from the floor at the Annual Meeting, if endorsed by two members of the Association.

After a brief discussion Dr. M. S. Goldstein, seconded by Dr. C. E. Snow, moved that the Association accept this revised version of Article V of the Constitution; the motion was carried unanimously.

The Executive Committee's next proposal, to amend Article II to provide for two vice-presidents (rather than one), provoked some brisk discussion and was tabled by the membership following the motion of Dr. J. W. Gruber, seconded by Dr. R. W. Ehrich. According to proper constitutional procedure both this and the preceding proposed revisions of the Constitution had been discussed at the last Annual Meeting and the essence of the discussion circulated to the whole membership together with the revised versions drafted by Dr. Stanley M. Garn and other members of the Executive Committee.

Having been charged with considering methods of appointing editors and associate editors for the Journal, the Nominating Committee, with Dr. W. W. Howells (Chairman) as

spokesman, presented the following recommendation, to serve as policy for the future:

"That the selection and appointment of Editors and Associate Editors of the *American Journal of Physical Anthropology* be vested exclusively in the Executive Committee of the Association (with the help and advice of the Editor in the selection of Associate Editors), the appointments to be made at the convenience of the Executive Committee; and the terms of said appointees to be as follows: Editor, 6 years; Associate Editors, 4 years."

On the motion of Dr. Robert White, seconded by Dr. C. S. Coon, this recommendation was adopted by the Association's membership.

The reports of the Treasurer and of the Auditing Committee were read and accepted.

TREASURER'S REPORT

Prudence Bond			$ 100.00
U. S. Savings Bonds (maturity value)			3,000.00
			$3,100.00
Bank balances, March 18, 1952		$3,240.86	
Receipts:			
Dues	$1,172.55		
Foreign postage paid	6.00		
Sale of STUDIES IN PHYSICAL ANTHROPOLOGY	16.00		
Receipts from participants at Annual Dinner	212.25		
		$1,406.80	
			$4,647.66
Expenditures:			
To Wistar Institute (subscriptions)	$ 689.00		
To Wistar Institute (proceedings)	76.70		
To Wistar Institute (programs)	78.32		
To Bertram Kraus (Newsletter)	50.00		
* To participants in Symposium on the Back at N. Y. Academy of Sciences	150.00		
* To N. Y. Academy of Sciences for meetings and smoker	220.00		
* To N. Y. Academy of Sciences (dinner)	517.00		
* Name tags and flowers (N. Y. meeting)	19.00		
Secretarial expenses	171.58		
Mailing for foreign members and express	6.50		
Bank charge	.25		
		$1,978.35	

* Symposium on the Back and other costs of New York meeting made possible by a generous grant of $700.00 from the Wenner-Gren Foundation for Anthropological Research. See Treasurer's Report for 21st annual meeting.

Bank balances, December 26, 1952:

Savings account	$2,000.00
Checking account	669.31
	$4,647.66

December 26, 1952
Respectfully submitted
J. LAWRENCE ANGEL, Treasurer

Certified to be as stated above.
December 27, 1952
G. E. ERIKSON
E. C. SENSENIG
Auditing Committee

The Treasurer announced that the Association had applied for and received from the Bureau of Internal Revenue the tax-exempt status of a non-profit organization. Gifts to the Association are now properly deductible in the givers' income tax returns.

Dr. W. W. Howells, Editor of the AJPA, reported that volume 10 of the Journal contained 40 articles and brief communications, and 9 book reviews. Twenty articles submitted had not been accepted. He pointed out that, as usual, the majority of authors in this volume were not members of the Association, which was due this year in great measure to the number of articles submitted from abroad. He expressed his thanks to Doctors Angel and Thieme, to the former for having served as book review editor during the year, and to the latter for assuming this work for the future.

In outlining current good relations of the Association to other organizations, president S. L. Washburn stressed the present cooperation with the AAA, especially as Dr. Sol Tax takes over leadership of the American Anthropologist, and announced the recommended appointment of Dr. T. Dale Stewart to represent the Association on the National Research Council.

Reporting on the Yearbook, Dr. William L. Straus, Jr., announced that it was in press. He praised the able energy of his collaborator as editor, Dr. Gabriel Lasker, then absent at the AAAS meetings where he was serving as Secretary of Section H.

Dr. W. M. Krogman announced that the Wenner-Gren Foundation Seminar in Physical Anthropology would be held in

June, 1953, at the invitation of Dr. H. M. Marjerison of the Forsyth Dental Infirmary for Children in Boston, Massachusetts. Dr. Edward E. Hunt is in charge of local arrangements. Doctor Krogman described the week's program as a development of the ideas which he had presented at the Ann Arbor meeting of the Association in 1951 on "the role of physical anthropology in medical and dental research." The meeting will bring together personnel in the clinical fields of orthopedics, pediatrics, oral surgery, orthodontics, prosthodontics, as well as physical anthropology, anatomy and embryology, genetics, biometrics, and nutritional physiology. Thanks are due to those suggesting participants in this good cross-section of personnel.

The Nominating Committee, Dr. W. W. Howells and Dr. R. White, presented the following nominees: for President, 1953–55, Dr. William L. Straus, Jr.; for Executive Committee, 1953–56, Dr. T. Dale Stewart. They were elected unanimously.

The Resolutions Committee submitted the following report, which was passed immediately:

REPORT OF THE RESOLUTIONS COMMITTEE

1. Be it resolved that the Association hereby expresses its gratitude to Dr. Froelich Rainey, and the staff of the University Museum, for their generosity in making available the facilities of the University Museum for the annual meeting.

2. Be it also resolved that the Association expresses its appreciation to Dr. Alfred Kidder, II, for his effort and care in making all the necessary arrangements at the University Museum.

3. Be it further resolved that the Association extends its thanks to the Department of Anthropology, University of Pennsylvania, and to its chairman, Dr. Loren C. Eiseley, for their hospitality to all the members of the Association at this meeting.

4. Be it also resolved that the Association expresses its thanks to the local committee, especially Drs. J. Lawrence Angel and Neil C. Tappen, and to the Museum assistants, for their efforts in making arrangements and facilitating registration at the University Museum.

5. Be it also resolved that the Association expresses its gratitude to Dr. William A. Laughlin for arranging the Symposium on Methods of Determining Significant Degrees of Relationship.

6. Be it further resolved that the Association expresses its gratitude to Dr. Josef Brozek for arranging the Symposium on Measuring Nutriture.

7. Be it still further resolved that the Association extends its warm appreciation to Drs. Gabriel W. Lasker and William L. Straus, Jr., for their work as editors on the Yearbook of Physical Anthropology.

8. And be it also resolved that the Association extends its appreciation to the Wenner-Gren Foundation for Anthropological Research, and its Director of Research, Dr. Paul Fejos, for its continued support of the Yearbook of Physical Anthropology and the Summer Seminar.

9. And be it finally resolved that these resolutions be incorporated into the minutes of these meetings and that they be published in the Proceedings of this Association.

Respectfully submitted,
E. S. C. Handy
F. Clark Howell

The twenty-third annual meeting was announced by Dr. Stanley M. Garn, Chairman of the Local Committee, as arranged for the spring of 1954 at the Fels Research Institute for the Study of Human Development, Antioch College, Yellow Springs, Ohio.

The scientific part of the program consisted of the following papers:

1. *Cephalo-facial growth in cleft lip and/or cleft palate children.* Richard M. Snodgrasse, Temple University School of Dentistry.

Ecto-oral facial growth of 33 cleft lip and/or cleft palate White children was studied at the Philadelphia Center for Research in Child Growth. A series of 19 facial measurements on each child together with his (her) stature, weight, and chronological age were compared with those of his peers in dental eruption stage by use of the Hellman S. D. graphs. The same principle was employed in comparing head length, head breadth, auricular head height, stature, and weight with that of a child's chronological age peers (Gray and Ayres' series). Dental eruption age ranged from IIA to IVA; chronological age from 2: 3 (i.e., 2 yr. 3 mo.) to 18: 0. The range given by M $\pm$ 1 S. D. was considered (following Hellman) an acceptable norm for satisfactory facial dimensions. Tabulation of the indices of abmodality (x–M./S. D.) leads to the conclusion that cleft lip and/or cleft palate children, as represented by this sample at least, tend to be characterized by generalized growth retardation. Twelve of the 26 measures were significantly small, $P = .05$, and 6 of the 26 — all involving facial depths (chiefly midline A-P) — were significantly small at $P = .01$. Contrariwise, dental eruption age appears skewed toward earlier than average while skeletal age (hand skeleton) appears

negatively skewed. Such indication of aberrant growth and development in children thus affected may be of service to the surgeon, the prosthodontist, the speech therapist, and the pediatrician in planning treatment.

2. The topology of the human premaxilla. Charles R. Noback and Melvin L. Moss, Department of Anatomy, College of Physicians and Surgeons, Columbia University.

The persistence of the labial lamina of the premaxillary bone in the human adult remains a confused problem for both anatomists and physical anthropologists. A critical review of the literature leads to the probable conclusion that the labial lamina of the human premaxilla persists in the adult without operculation by the maxilla. This review of the pertinent data may help bring the question nearer to clarification in the minds of those dealing with its implications.

We must consider morphogenesis in addition to morphology. The methodology is properly embryological and not comparative. Two key points must be observed. The first is that no material younger than 6 to 7 weeks, nor older than 9 weeks (fetal age) may be properly utilized, the onset of ossification occurring at the former and the union with the maxilla at the latter. Any studies on later material will necessarily miss this key stage and so invalidate itself.

The second key point is terminological. Confusion exists between the terms osseous process and the embryonic masses of the branchial arch region also termed process. This has led to confusing the contribution which the embryonic maxillary process makes to the formation of the premaxilla with the existence of an osseous maxillary process labially covering the premaxilla in the adult. A further confusion exists between the contributions of the maxillary process to the soft tissue of the upper lip and those to the osseous structure itself.

3. Hereditary traits of the mandibular premolar teeth. Bertram S. Kraus, Department of Anthropology, University of Arizona.

Although it has long been postulated that the structural variations of the crown surfaces of the dentition are heritable, only one common morphological trait, Carabelli's Anomaly, has been genetically analyzed. We have studied casts of the mandibular first premolars of 800 persons. Seventeen morphological traits of the crown surfaces have been isolated, described, and classified; their independent variability has been established; and their heritability has been demonstrated. The genetic mechanism involved in each instance remains to be investigated.

Two of these traits are presented here. One is the number of lingual cusps or cusplets. A lingual cusp is defined as having an independent apex, however slight, located on the lingual moiety of the premolar. There may be only one, the deuteroconid, or as many as 5. Monozygotic twins show strict concordance in the number of lingual cusps. Dizygotic pairs show discordances in expected frequencies. There are indications of significant differences in the distribution of aspects of this trait among separate breeding populations.

The second trait concerns the central occlusal ridge of the protoconid. The ridge may take a straight uninterrupted course throughout its entire length (from apex to sulcus or deuteroconid), or it may divide partway down its course and present a bifurcated appearance. These two variations are heritable, as

shown by twin studies and by pedigrees. In the samples of populations available for study, significant differences in relative frequencies of the two aspects were noted between Mongoloids on the one hand and Caucasoids and Negroids on the other.

Statistical analysis of the total sample, involving all 17 premolar traits, indicates that each trait acts as an independent variable relative to all the others.

4. Variation in caries frequency by sex and site. Frederick P. Thieme, Department of Anthropology, University of Michigan.

Variation in caries frequencies was discussed in light of data gathered from a sample of adult Puerto Rican males and females. The findings indicate that significant variation occurs by sex and by site in Puerto Rico, and probably for all populations. By sex, the rate of loss for groups between 20 and 45 years of age is 0.29 for males compared to 0.58 teeth per year for females, with both groups having substantially the same number of non-carious teeth at age 20. As for site in the dentition, lower anterior teeth are significantly free from caries compared to upper anterior ones (I-1, I-2, C). Also, upper molars have lower caries rates than lower molars. In general, all the lower teeth anterior to PM-2 are less attacked than the similar upper teeth, but the situation is reversed with the upper teeth being better in the molar group. No difference occurs at PM-2.

These patterns were analyzed according to differences in nutrition, racial background and geographical region of residence. Although the details of the differences are altered by nutrition, race and residence, the over-all consistency remains as an apparent human characteristic probably related to a basic similarity in all groups compared.

5. Suture closure in the chimpanzee. George A. Harley and E. L. Schuman, Peabody Museum and School of Dental Medicine, Harvard University.

A collection of 291 chimpanzee crania from northeastern Liberia has been arranged in 9 main age groups on the basis of tooth eruption and tooth wear; the groups subdivided for sex. The sex criteria are discussed. Seven males exhibited gorilloid crests. A preliminary comparison of the skulls thus grouped has shown evidence of certain trends in the suture closure pattern. The lambdoid suture is the first to close, the zygomatic is the last. The coronal and the occipito-mastoid may remain not entirely closed until well past maturity. The infra-orbital persists almost as late. It was noted that certain sutures which are shown to stay open throughout most of the growing period, were thickened, or raised, beginning at an early age. The opinion is expressed that this may be due to unusual stresses. Some sutures tend to close somewhat earlier in the female. Probable reasons for both early and late closure are discussed, with special reference to stresses imposed upon the bony structure supporting the teeth, and to the attachment of muscles which impose these stresses.

6. Duration of growth in primates. James A. Gavan, Yerkes Laboratories of Primate Biology, Orange Park, Florida.

In a long series of papers Schultz has repeatedly stated that in the series monkey, anthropoid ape, and man the duration of the total growth period (conception to

adulthood) has increased, but that in man the increase in the postnatal growth period is relatively greater than in other primates. This question is reexamined in the light of more recent data for the chimpanzee.

The total growth period was subdivided into the prenatal period (conception to birth), infancy (birth to completion of deciduous dentition), childhood (completion of deciduous dentition to puberty), and adolescence (puberty to adulthood). The chimpanzee and macaque data, although based on small samples, are semilongitudinal whereas the human data are strictly cross-sectional.

When expressed in months the total growth period and each of its subdivisions are longer in man than in the chimpanzee, and longer in the latter than in the macaque. However, contrary to Schultz's conclusions, when each subdivision is expressed as a per cent of the total, man and the chimpanzee are almost identical, and both differ greatly from the macaque.

From monkey through anthropoid ape to man there has been an absolute increase in the duration of the total growth period. In relative terms the timing of events within the total growth period is the same for chimpanzee and man, and both differ from the monkey.

7. *Studies in physiological anthropology. III. The age of onset of menstruation of the Alaskan Eskimo.* Victor E. Levine, Creighton University School of Medicine, Omaha, Nebraska.

An opportunity was afforded in 1948, while on a grant from the Office of Naval Research, to study the age of onset of menstruation at Pt. Barrow, Alaska. Of 122 females investigated, the percentages for each year are: 9–10, 0%; 10–11, 0.82%; 11–12, 0%; 12–13, 9.84%; 13–14, 25.41%; 14–15, 36.06%; 15–16, 17.21%; 16–17, 9.02%; 17–18, 1.63%; 18–19, 0%. The mean for the series is 14.42, and the standard deviation 1.20.

Compared to a series of 300 Nigerian females (Ellis, R. W. B., British Medical Journal, 1950, 1, p. 85) of which the mean age of menarche was 14.22, the difference between the means of the Nigerian and the Eskimo series is 0.20, and the standard error for both is 0.114. Since this difference is only 1.75 times the standard error, it may be considered below the level of significance.

An English series of 470 females (Ellis, R. W. B., Edinburgh Medical Journal, 1947, 54, p. 269) gave a mean of 13.73. The difference between the means of the English and the Eskimo series is 0.69, and the standard error for both is 0.113. This difference is 6.1 times the standard error, and is statistically significant.

The Nigerian study was made on negro females in the township of Lagos, West Africa, situated on a coastal island in latitude 6°27′, approximately 450 miles north of the equator, and possessing a tropical climate. The present study was made on Eskimo females in the Arctic at Pt. Barrow in latitude 72°, and possessing an arctic climate. The results of these two studies indicate that neither climate nor race markedly affect the age of onset of menstruation. Physiological functions as expressed by menarche, basal metabolic rate (Levine, V. E., Federation Proceedings, 1942, 1, p. 121) and blood pressure (Levine, V. E., Journal of Biological Chemistry, 1939, 128, p. LIX) are not dependent on race.

8. The development of some secondary sexual differences in terms of CR/D. Božo Škerlj, University of Ljubljana (Yugoslavia).

The reference sample are healthy secondary and high school students (1097 boys and 1613 girls) of Ljubljana (Yugoslavia). The growth period under consideration is 11 to 23 years of age. Eleven measurements were taken and thereof 9 indexes derived.

The measurements and indexes show that measurable sex differences develop during that period partly in a very definite way: Greater absolute head length and breadth as well as Lorentz' spiroindex, in boys, relatively broader hips and stouter thighs, in girls, are significantly different during the whole period under consideration. That means that these characters develop sexually differently even before that period. The cephalic index and the relative waist girth are, broadly speaking, sexually indifferent during that whole period. Stature, Rohrer's index, bi-acromial width, relative bi-cristal width, absolute chest and waist girths, as well as the relative thigh girth become sexually significantly different during that period. Absolute bi-cristal and bi-trochanteric widths as well as relative chest girth become sexually indifferent characters after 18 years of age. Weight and relative bi-acromial width change the significances of their differences.

Further similar investigations, elsewhere in the world, seem to be indicated to improve our knowledge regarding the development of sexual differences which might be different also between social, ethnic, constitutional, and racial groups.

9. Brain morphology and taxonomy. C. J. Connolly, Department of Anthropology, Catholic University of America, Washington, D. C.

Brain morphology at the present time plays a very small role, especially on this side of the Atlantic, in the interpretation of the relationship of the various groups of primates. From an early period when too much was expected from this source, we have come to a period when less is expected than is justified by the established facts. At most we have a reference to cranial capacities and the body weight-brain relationship. Yet there is much available information on brain morphology which can throw light on the relationship of various groups of primates and there are well established frequency differences in the form and fissuration of the brain in human races.

External brain morphology in general reflects the relationship assigned to groups of primates by taxonomists. This applies to the subfamily category, frequently to the generic and sometimes to the species. In some cases where taxonomists disagree, brain morphology can contribute to the solution.

Endocranial casts reveal very closely the shape of the corresponding brain. Although representation of the fissural pattern is generally meager on the endocasts of modern man, it may be pronounced in fossil hominids; also in the chimpanzee and almost always in the gibbon and lemur. The importance of these facts for the interpretation of fossil finds should not be overlooked. But caution has to be exercised as illustrated by the fact that at least one alleged hominid character assigned to *Pleisanthropus* is really not a specifically hominid character, but occurs also in the anthropoid brain.

10. Organic evolution and man. Dudley J. Morton, M.D.

Locomotion, an organic interaction with a single environmental factor (gravity) and governed by the laws of mechanics, is a general characteristic of the animal division of organic life. In the greater density of water, the action of gravity is *indirect*, as resistance; in air, it is *direct* as bodyweight. Vertebrates are identified as a group in which ever since their primitive pattern was laid down in a segmented spinal structure and bilateral myotomes, their bodyform has been composed predominantly of *locomotor* tissues (skeletal framework and musculature), and its over-all design represents the aggregate pattern of those locomotor structures.

In aquatic life, evolutionary changes culminated in the fusiform, heavily-muscled bodies of the rapidly swimming fishes. With emergence to land life, the predominance of locomotor structures persisted. Also, remodelling of the paired fins to strong weightbearing limbs made them increasingly important elements in body design, especially as different methods of interaction with gravity with corresponding changes were imposed by various locomotor habits.

Nowhere in Nature is the specific influence of gravity in the molding of vertebrate bodyform more patently revealed than in the late and unique sequence of adaptive modifications which created mankind. In that sequence is disclosed the course by which, from the primitive *quadrupedal* primate, man's body stature was fashioned with its erect bipedism, the manipulative strength and mobility of his arms and hands, straightening of his legs and weightbearing specialization of his feet, as the essential physical provisions for his intellectual development.

11. Hair structure as revealed by polarized light. P. B. Candela, San Bernardino, California. (Read by S. M. Garn.)

The importance of the study and classification of hair in the investigation of human and racial origins has been recognized since the earliest beginnings of physical anthropology.

The following preliminary report, based on a 10-year study of the appearance of hair in polarized light, deals with a new approach, which appears to furnish new information regarding the internal structure of hair, and holds out much promise for anthropological, genetic, and perhaps even medical applications.

When a hair is viewed between the two prisms of a polarizing microscope, it is invested with glowing colors, often resembling neon lights. Slides are shown, illustrating the two contrasting types. In the first, the hairs appear a light yellow-orange, while in the second, the hairs exhibit a colored central cylinder, bounded by colored bands. Numerous modifications of the latter occur in sharply kinked hairs, in which bizzare mosaic patterns are seen.

The simple yellowish appearance is interpreted to be the basic background color, upon which, in many hairs, colored cylinders, bands and spots are superimposed. These cylinders, bands and patches are believed to be reflections of discontinuities in the internal structural arrangements of the hair, produced by varying intensities and configurations of internal stress. Thus the colorful and sometimes complicated designs are seen to be nothing more than the familiar "stress pattern," such as is studied routinely in many branches of industry.

Experimental and observational evidence for this belief is presented briefly, and illustrated with color slides.

12. Classification of the catarrhine primates. William L. Straus, Jr., Laboratory of Physical Anthropology, The Johns Hopkins University.

Some past and present classifications of the Old World Anthropoidea, or Catarrhini, are discussed. Certain taxonomic problems that have arisen as a result of recent discoveries of fossil catarrhines, notably the Australopithecines of South Africa and the Early Miocene hominoids of Kenya, are considered.

It is suggested that (1) the basic criterion of the family Hominidae be an erect, bipedal posture, and (2) that of the genus *Homo*, a degree of cerebral development resulting in the production of a culture, as evidenced paleontologically by the presence of manufactured tools.

13. The reconstruction of the skeleton of Skhul V. Charles E. Snow, Department of Anthropology, University of Kentucky, Lexington.

During the summer of 1951, the well preserved skeleton, Skhul V (upper Paleolithic age, Interstadial Würm I and II), excavated from the Mugharet es Skhul Cave on Mt. Carmel (1935–37), was reconstructed. This process was simply additional to that accomplished by Dr. Theodore McCown under Sir Arthur Keith's supervision.

The marked skull unconformity (apex of Parietals) was eliminated by cutting apart the numerous fragments constituting the entire frontal bone and much of the left parietal, and restoring the original, somewhat lower rounded contours. The distorted, smashed-up face was freed, by a series of drill holes, realigned and reset upon the articulating well preserved mandible. All of the teeth of both jaws were carefully reset, matching the mutually worn (interproximal) tooth facets. Restoration of the missing nasal and bordering maxillary sections was accomplished, first by using plasticine. When existing examples and all other guides, including departmental advice, were carefully consulted, examined and followed, the missing facial parts were replaced with albastone. Filling-in and touching-up the tip of the left mastoid and left occipital condyle as well as other small holes, completed the reconstruction of the cranium.

The stone-bonded right hip joint was carefully separated, freeing the well-preserved upper shaft portions of the right femur. With this and the distal end of the left member, it was possible to cast and restore opposite side duplications, providing reliable approximate reconstructions of both femora. Working from the perfectly preserved tibia bones of Skhul IV, a reconstructed head and distal extremity were fashioned to complete the very large, right tibia of Skhul V, including a well-formed squatting-facet.

Not only were the bones embedded in travertine, but the numerous fragments broken before the cave waters recemented them together, were bonded and/or filled with some extraordinarily hard siliceous deposits. The ordinary small electric circular saws, emory wheels, dental drills and burrs proved ineffective on these harder mineral substances. Patient trial proved that the steel alloy carbide-tipped drills were the most practical equipment with which these hardest cementing-bonds could be cut.

Although the forearm of Skhul V bears an extremely short relation to the upper arms (Humero-radial Index about 66.6, Humero-ulna Index about 73.4), the maximum length of the upper arm and all leg members are very great and indicate

an estimated stature of over 6 feet. This is truely one of the great men of the Old Stone Age in the Middle East.

Some of the reconstruction steps were depicted by means of colored slides.

14. Interpretations of the Hotu skeletons. C. S. Coon and J. L. Angel, University Museum of the University of Pennsylvania and the Daniel Baugh Institute of Anatomy of the Jefferson Medical College.

Attempts to determine the exact date of the Hotu skeletons have not yet succeeded. Recent Russian evidence, that the Caspian may have been flooded to above the level of the caves during part if not all of Würm times, reduces the likelihood of a 4th glacial date, and increases the possibility of either an early postglacial or third interglacial time locus. The flint industry, while inconclusive, points to the later rather than the earlier period, while the fauna could have been present in either. The entire problem is a complex one, particularly in view of the multiplicity and differentiation of strata both over and under the skeleton.

Stresses of a hunting existence show in the three Hotu skeletons in bony crests and ligament osteophytes (vertebral bodies rimmed, plus collapsed 5th lumbar-1st sacral disk in the strong, 27-year-old female no. 2, thumb-wrist arthritis in 37-year-old female no. 3, and foot arthritis in rugged 40-year-old male no. 1) greater than on modern people of similar age, and also in lower extremity traits grouped under the term "bent-knee gait" and metrically similar to Upper Paleolithic and other primitive hunting populations. Number 2 has a tall, linear and desert-adapted body build, similarly narrow and high skull vault and very low broad face. Number 3 has the stocky, short, and massive build found in arctic peoples, with almost brachycrane skull vault and appropriately Cro-Magnon-like low and wide face. Number 1 is tall and robust with a largely restored skull, narrow, and probably quite long and high, having an exceedingly sloping and long forehead, massive browbridges, and a high and beaky face with sharply tilted chewing plane, all together comparable to Skhul no. 4 and to the extreme of Vallois' Proto-Iranian tendency described at Chalcolithic Sialk.

Though similarities in certain features, such as the chin and mouth area, suggest that these formed one inbred population the extreme heterogeneity parallels the earlier Palestinian Neanderthaloids and the possibly contemporary skeletons from the Chou Kou Tien Upper Cave. Hotu and Chou Kou Tien thus suggest the kind of microevolutionary changes which must have marked the whole sweep of Central Asia when freedom from glaciation allowed free population movements.

15. Adaptive change and race formation in the aboriginal New World. Marshall T. Newman, Division of Physical Anthropology, U. S. National Museum, Washington, D. C.

Coon has suggested that the more recent adaptations in man took place largely in body size and proportions, while the surface traits such as pigmentation and hair form were more resistant to environmental pressures. In the aboriginal New World, body size and proportions show high variabilities in comparison to the "Mongoloid Wash" surface traits (Hooton). That the high variability traits are the result of adaptive alterations after reaching the New World is demon-

strated by the geographic patterning of their distributions. With several exceptions, notably the Eskimo, stature shows a progressive increase north and south from the equator. Sitting height, head size, and face size have the same sustained clines. These ecological correlations conform with Bergmann's Rule — that within wide-ranging species of warm-blooded animals, the subspecies in cold climates attain greater body size than those in warm climates. In body proportions, the relatively longer trunk and shorter legs of the Eskimo conform to Allen's Rule — that cold climate subspecies show a reduction of bodily appendages. Also the face becomes relatively longer and the nose narrower toward the extreme north and south.

Most of the classifications of aboriginal New World races are based largely upon differences in these measurements and indices. It seems erroneous, therefore, that these races are usually explained in terms of a separate migration from Asia to account for each one. Without denying that the New World was populated by successive movements of physically different peoples, it is likely that the classifiers' races are largely ecological races formed in the Americas.

16. The whole man as organism in nature and culture. E. S. C. Handy, Bishop Museum, Honolulu, Hawaii.

Anthropology is the science of man as a whole. Yet has any anthropologist studied one man wholly? This entails appraisal of (1) the organism, in terms of the functional systems of the body which are the instrumentalities of adjustment to environment; (2) the environment in terms of the specific elements or factors by means of which life is maintained; (3) the role of the individual organism, or person, both in relation to physical environment, and as a socio-cultural entity in its human milieu (family and community); (4) the interpersonal relations consequent upon role; (5) the character of the individual induced by role and relations within milieu; and (6) behavior peculiar to the individual as an integral organism having unique role, relations and character. All these must be considered not statically but developmentally, in terms of the whole life span. And the individual as organism and social entity, to be in focus, must be appraised against the background of specific physical heredity and socio-cultural heritage. Examples are drawn from (1) a Hawaiian fisherman-planter whose lifelong and daily identification with sea and soil dominates his body and his culture, and (2) a modern intellectual in fundamental ways divorced from earth, engrossed in mental preoccupations, whose tools are words.

PANEL DISCUSSION: MEASURING NUTRITURE

Arranged by Dr. Josef Brožek

17. Measuring nutriture: Some anthropometric implications. Josef Brožek, Laboratory of Physiological Hygiene, School of Public Health, University of Minnesota.

A quantitative evaluation of nutritional status (nutriture) involves also the use of anthropometric data. There is a pressing need for the standardization of procedures, design of adequate instruments (esp. skinfold calipers), and provision of valid norms.

For metabolic studies, the procedures of characterizing body build in terms of indexes (based on external measurements and gross body weight) or of Sheldon's "components" are not satisfactory. What is needed is the amount of principal tissues, a goal stated by Matiegka long ago (Am. J. Phys. Anthrop., *4*, 223, 1921).

The x-ray analysis of tissues, measurement of the thickness of subcutaneous fat by skinfold calipers, and data on limb circumferences and external dimensions of the bony structures may be used for *predicting* the volumes of the soft tissues (fat, muscle) and the bony mass. In the last decade, a striking progress was made in the analysis of body composition, *in vivo*, by biophysical (specific gravity) and biochemical (total body water and its fractions) methods, providing criteria needed by the anthropologist for correlational analysis and the computation of prediction equations.

While nutritional anthropometry is an *application* of physical anthropology, the new ideas and data will force rethinking of some of the *fundamental* concepts, including that of "body build." At the same time, the absence of needed information, e.g., on individual differences in bony mass, has become evident and should vigorously stimulate further research.

In metabolic investigations, the physical anthropologist operates as a member of an interdisciplinary team and is exposed to the salutary wind of fresh ideas and new techniques contributed by the whole gamut of sciences constituting human biology.

18. The problems of measuring obesity in chronic disease control programs. J. Wallace Rion, Division of Chronic Disease and Tuberculosis, U. S. Public Health Service.

Obesity has been called "America's No. 1 Health Problem" because of the observation, in life insurance data, of a positive relationship between death rates from degenerative diseases and total body weight above the average for a given height.

Since height-weight relationships give only crude estimates of the amount of body fat, they have certain limitations as the basis for a Public Health program designed to prevent or alleviate chronic disease processes. These limitations are:

1. In basic research into the specific nature of the interaction between obesity and chronic disease.

2. In studies of the relative importance of obesity in the complete causal nexus. This is extremely important in allocating limited public health resources to various activities.

3. In field programs for identifying obese persons, and in recommending the amount of weight to be lost.

In attempting to cope with these problems the Division of Chronic Disease and Tuberculosis has made a review of the development of the height-weight concept, and of available height-weight data for relatively large population groups.

Based on observations from earlier, small scale, insurance studies, the first large study of mortality by weight groups was included in the Medico-Actuarial Study of 1912. Standard height-weight tables in use today are based on data from this study. Later insurance studies attempted to refine measures of build by including other body measurements.

Data are presented showing height-weight relationships found in insurance studies, selective service examinations and recent multiple screening programs.

19. The reliability of serial measurements taken on children of different body build. Wilton Marion Krogman, Philadelphia Center for Research in Child Growth.

The first problem involved stability of build from year to year. The Wetzel Grids of 200 children (100 boys, 100 girls) aged 6: 6–14: 6 were examined, in two groups, below 10: 0, above 10: 0. In all we had 4 or 5 annual H–W observations. In the first group 30 boys and 28 girls traversed single or adjacent channels; 10 boys and 13 girls shifted two or more channels on the above side, and 7 boys and 6 girls two or more on the below side. In the second group 37 boys and 29 girls traversed single or adjacent channels, 14 boys and 17 girls shifted two or more on the above side, two boys and 7 girls two or more on the below side. Over-all 67% of boys, 57% of girls, were in single or adjacent channels; 24% of boys, 30% of girls, shifted two or more on the above side, 9% of boys, 13% of girls, two or more on the below side.

The second problem centered around the average increment, in the age period and for both sexes, in height, weight, symphyseal height, illiospinal height, shoulder breadth, chest depth, bicristal breadth, and bitrochanteric breadth. Then two smaller test-samples were selected: those whose channel ratings were between A_2–B_2, and those whose channel ratings were A_4–A_{10}. It was found that the increments in the first group more nearly approximated the averages of the entire group, while those of the second group were in excess of the average, but very erratically so. With increased weight serial measurements lose reliability, and directly in those dimensions where fat deposition is at a maximum, notably around the hip girdle.

It was concluded that anthropometry on such subjects must be accompanied by x-ray analysis of fat-muscle-bone ratios.

20. Subcutaneous fat and age changes in body form of women. Božo Škerlj, University of Ljubljana, Yugoslavia, Josef Brožek, Laboratory of Physiological Hygiene, University of Minnesota, and Edward E. Hunt, Jr., Forsyth Dental Infirmary, Boston, with the technical aid of Kung-Pei Chen, Walter Carlson, and Florence Benczyk.

The description of human constitutional patterns involves a differentiation between tissues which vary with age and those which remain relatively constant.

In the summer of 1952, 84 women were studied at the Laboratory of Physiological Hygiene, University of Minnesota. These women ranged from 18 to 67 years of age. The overall study was designed to evaluate changes in body composition, with special reference to the fat content, and paralleled with similar work on men (Fed. Proc. 11, 784, 1952). Subcutaneous fat was measured at 10 sites by spring calipers and the fat content of the body was estimated from specific gravity.

Three age groups were sorted out (18–30, 31–45, and 46–67). Pronounced age differences in the amount and distribution of soft tissues occurred. Physiques showing an abundance of soft tissue in the extremities and lower parts of the body decreased in the older groups, while women with considerable fat on the

trunk, breasts, upper arms, chest and trochanters increased. The normally proportioned form with moderate amounts of fat harmoniously distributed, became rare in the older groups, while harmoniously adipose forms increased.

The lean body mass in women is remarkably constant with age; yet the content and distribution of fat are more liable to change. Although the patterns of subcutaneous fat alter, and in most instances show an overall increase, the inner fat seems to increase more than the total subcutaneous fat. Perhaps the rate of accumulation of inner fat — a phenomenon quite inaccessible to traditional anthropometry — is one of the most useful criteria of aging for future nutritional and constitutional research.

22. Comparison of Negroid and White fat changes under desert heat stress. Paul T. Baker.

In June, 1952, a group of 21 Negroid and 45 White soldiers were measured in Virginia, prior to their departure for a 6-week tour of duty in the Arizona desert. They were subsequently measured at weekly intervals. Measurements used were: weight; mid-arm, shoulder, chest and waist circumference; subcutaneous fat of the upper arm, chest and waist (by skinfold calipers); and total percentage of fat in the body. In pre-desert measurements, both groups had the same mean stature and weight. The Whites had significantly larger chest and waist circumferences and twice the amount of fat. By the end of the first week in the desert, the Whites had gained in all torso measurements and in total body fat. After this time, there was a steady decrease in torso circumference measures and in amount of torso fat. Arm circumference and arm fat decreased continuously, without the initial first-week rise. Negroid measurements did not display the same increase in fat and circumference during the first week. Instead, a steady loss in fat was recorded for the full test period, while changes in circumference were erratic. Final measurements showed that Negroids lost 25% of their original body fat while Whites lost 13%. Contrary to expectations, weight losses did not accompany body changes in either racial group.

23. Measurement of body fat by air displacement. Ralph J. Wedgwood and Russell W. Newman, QM Climatic Research Laboratory, Lawrence, Massachusetts.

The most practical and accurate method of measuring total body fat is by assessment of specific gravity. All direct specific gravity data are at present obtained through total immersion of the subjects in water. This technique requires cumbersome and non-portable apparatus, a period of subject training before reliable results can be obtained, a careful measurement of the residual air in the lungs, and is inapplicable to the very young or the infirm.

A method which avoids or minimizes the disadvantages of water immersion is that of substituting air displacement for water displacement. A short motion picture showing the apparatus being used on two subjects was presented. The general theory of the measurement of air displacement by electrical means, the methods of calibrating the volumetric cylinder, calculation of body fat on two subjects, and comparison with body fat obtained by skin-fold measurements were shown.

SYMPOSIUM: METHODS OF DETERMINING SIGNIFICANT DEGREES OF RELATIONSHIP

Arranged by Dr. William S. Laughlin and co-sponsored by the American Anthropological Association

24. The genera of New World primates. G. E. Erikson, Department of Anatomy, Harvard Medical School.

Our fundamental ignorance of the biology of the New World primates is reflected in the taxonomy of the group, which is a chaos of synonymic and conceptual snarls. This chaos not only reflects our ignorance but is a large factor in perpetuating it. This cycle must be broken by adopting a working taxonomic scheme of the genera that is frankly provisional but designed to provide categories that are morphologically homogeneous and of a minimum of ambiguity in nomenclature. It will serve its full purpose if it expedites the studies needed for its confirmation or revision.

Such a classification of the genera of New World primates is here proposed for the consideration of anthropologists, with analytical charts and diagrams designed to clarify some of the perplexing issues. It has been found preferable to adopt small homogeneous categories, some of which may in the light of fuller knowledge require recombination, than to force an unnaturally simplified taxonomy that confuses the investigator through the disharmony of its generic constituents. In accordance with this principle the marmosets, rather than being grouped into two or three large and demonstrably heterogeneous genera, are subdivided into 6 *(Callithrix, Cebuella, Leontocebus, Tamarin, Marikina,* and *Oedipomidas)* though the last three, thus separated for investigation, may prove to deserve only subgeneric distinction. Similarly, the saki-urakari complex constituting the Pitheciinae is subdivided into three genera *(Chiropotes* and the more commonly accepted *Pithecia* and *Cacajao)* rather than combining them all under one genus as the annectent nature of the first might permit.

25. Fossil man: Interpretation of morphology. F. Clark Howell, Department of Anthropology, University of Chicago.

A key problem in human paleontology is the interpretation of morphological features of extinct hominids and other primates. Phylogenetic relationships are determined by morphological comparisons but frequently the significance of anatomical features so compared is but poorly understood.

The Sylvian crest is such a case. This is a thin ridge of bone on the anteroinferior portion of the internal wall of the parietal bone. Present, but poorly known, in modern man, it is well-developed in Pithecanthropus and Sinanthropus, less well marked in some of the Neanderthals (where studied). Four interpretations for the structure have been offered: (1) It fills an otherwise vacant space in the Sylvian fissure due to deficiency of cortex (Weidenreich); (2) it acts as a supporting buttress (Schwalbe); it is due to ossification induced by the brain-enclosing dura mater covering it (Hyrtl); (4) it serves as "an adaptation for transmitting the thrusts between the temporal muscle and the skull" (Keith).

The split-line technique shows that where present in modern man, the structure is organized bone, the split-lines running postero-superiorly. Other work reveals that such lines are not due to chewing pressures from mastication or to the dura which is here merely a loose covering. On the external wall of the vault, this same area is covered by deep fibers of the temporal muscle (medial portion). The greater wing of the sphenoid is thickened bone and this apparently extends internally as the Sylvian crest. The crest appears then to be related to the temporal muscle fibers which have the same general direction and, when well-developed, place the area under considerable strain. The split-line technique shows that the area is stressed and not then a simple filling in of bone. Muscle excision on laboratory animals allows this conclusion to be tested experimentally, and since rare temporal muscle paralysis occurs in man, clinical data can be used with man himself as a test case. This is but one of many problems of structural morphology which need clarification if human paleontologists are to better understand Man's Place in Nature.

26. Race and culture: the social biology of mixture. J. Lawrence Angel, The Daniel Baugh Institute of Anatomy of the Jefferson Medical College, Philadelphia.

Mixture has been held a major engine for cultural advance since it has accompanied each step in growth of the great civilizations. Yet elsewhere mixture may be linked with social confusion. Which is the significant relationship?

Recent syntheses of brain function (Hebb, Penfield, Bard and Mountford, Ischlondsky, Cobb) stress: human infant learning over a myriad cortico-diencephalic circuits is much slower than in smaller-brained animals, with consequent need for greater loving care; that change of sensory stimulation (below the pain level) is felt as pleasure, especially change from any repeating stimulus. Alternation between security and exploration early in life teaches enjoyment. Thus to healthy adults variety of experience is pleasant, response to intermittent difficulties is flexible and overcompensating, and cooperation (as well as competition) is satisfying. The opposite should apply to rigid people. Statistically validated observations on interaction (Chapple, Poffenberger) check these inferences and fit genetic differences in mental functioning (twin studies).

Long-term associations between biological and cultural changes in Greek populations can be tested with χ^2. Rate of biological change is inversely related to population density. Racial, ethnic, and cultural variety and fusion run parallel and biological variability correlates with rises in culture level. Improvement in health has a cultural origin but increases biological energy available. Genetic recombination is worth examining but hybrid vigor seems irrelevant. Psychological reaction to mixture remains as the key factor: contrast proto-Communist Sparta with more flexible Athens.

27. Social structure and population differences. Frederick P. Thieme, Department of Anthropology, University of Michigan.

That social structures may be responsible for many of the biological differences that occur in human populations was discussed in light of two specific examples. Many anthropologists have previously concerned themselves with this relationship

and it never has been seriously doubted, however, it awaited the development of knowledge about human genetics to be more precisely quantified.

As examples of recent more exact descriptions, the relationship between Puerto Rican attitudes about skin color and the patterning of gene distributions on that island was given to show how cultural attitudes may set up non-random mating situations. Or to put it in another way, relatively homogeneous genetic groups can be sorted out of the total Puerto Rican population by dividing the sample into skin color groups. In addition, it was stated that skin color is much more efficient in this respect than nose shape, hair form or lip characteristics, or any other common phenotypic feature which varies appreciably in that island's population.

In another example, the findings of Schull on the frequency of consanguity in Nagasaki, Japan, indicate that Christianity may affect mating structure as to importantly differ the inbreeding coefficient between Catholic and non-Catholic Japanese. Here again, the cultural conditions modify mating behavior which in turn sets up population differences. In general, as random mating for man is likely only when his society is unstructured, anthropologists must study social structure in order to measure the effects of non-random mating.

28. The anthropologist and population genetics: a discussion of ethnographic method. R. H. Osborne, Columbia University. (No abstract.)

29. Statistical analysis. W. W. Howells, University of Wisconsin.

It should be a major concern of statistics in physical anthropology to provide methods of estimating relationship from whatever data are being used; however, statistics have actually been used almost exclusively only to test the significance of differences, a very different thing. In fact, physical anthropology is far behind biology and genetics, and even such subjects as sociology, in the applications of statistics. This state of affairs is probably due largely to two causes: the accident of personalities (i.e., the early dominance in this country of Hrdlička); and the 19th century development of methods in which the few original traits used to describe individuals and distinguish "races" became multiplied enormously without the establishment of relationships among traits, or understanding of their basic significance, so that populations were represented only by a large number of undigested averages and the individual was unrecognizable.

The Coefficient of Racial Likeness was the one attempt to change the situation, but this actually remained a test of the significance of difference, not a measure of likeness. What is needed is a system which will: (1) handle more than one measurement or trait, (2) take account of the variance of each measurement, and (3) take account of the correlation of characters. Such a system now exists in multivariate analysis, which covers such related techniques as analysis of variance and covariance, factor analysis, discriminant functions, generalized distance and canonical variates.

30. Methods of determining significant degrees of relationship. A summary. William S. Laughlin, Department of Anthropology, University of Oregon.

Since anthropology may be characterized as a comparative study of man, the search for objective methods of determining significant degrees of relationship

in its data should characterize much anthropological research. A continuing inquiry into the s gnificance of traits employed in studies, sensitive and non-coercive techniques of quantifying them, and intelligible standards or methods for evaluation of these comparative studies appears necessary, unless preconceived linear and typological concepts such as that exp essed in the Great Chain of Being are considered satisfactory for the organization and evaluation of data.

An examination of past physical anthropology reveals a tendency for vogues in interpretation to dominate the field. The first major system of explanation was derived from ideas related to the Great Chain of Being. Accordingly, much emphasis was placed on inventorying nature and little on understanding the processes of diversification. The second major system arose with recognition of the concept of evolution but is characterized in the United States by the belief that Evolution took place "somewhere else." As a consequence, differences between earlier and later populations in New World sequences were routinely attributed to migration from the Old World with little or no change having taken place here. The third vogue in interpretation consisted of the excessive resort to hybridization between original prototypes to explain the various combinations of traits in populations. The 4th vogue was the habit of using mutation to explain an unusual occurrence of traits or departure from expected type. All 4 of these vogues rested upon a belief in ideal prototypes and therefore stand in marked contrast to contemporary population analysis.

There is an increasing use of experimental and clinical evidence to determine the functional significance of traits, and a greater use of statistics appropriate to the nature of the problems involved. Much more emphasis is placed upon determining the mode of inheritance of traits and their functional correlates. The recognition that cultural processes inhibit or enhance the exchange of genes, both inside and between populations has facilitated the use of population genetics and also provided more information concerning contact between peoples of use to ethnologists. More attention is also given to processes, such as genetic drift, which may contribute to internal change in populations. It is now possible to select objective systems of analysis and interpretation and thereby to be free from the stultifying limitations of historical vogues in interpretation.

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Overeating, Overweight and Obesity. Edited by Robert S. Goodhart. The National Vitamin Foundation, New York, 149 pp. 1953. $1.50.— This publication of the National Vitamin Foundation summarizes recent research and contemporary thinking about obesity, that is, excess fat. No new "cause" of obesity is propounded: the majority of the papers deal with fat as a simple matter of overnutrition, and some of the reasons why people overfeed. Somewhat dissenting votes to the over-simplified explanation of compensatory overeating come from Hunt, Fry and Peckos of the Forsyth Dental Infirmary. A. W. Pennington of the DuPont Company suggests high-fat high-protein low-carbohydrate diet based on more sophisticated assumptions about excess fat than the usual. Of especial interest to physical anthropologists are the chapters by Louis Dublin, Ancel Keys, and the Hunt-Fry-Peckos contribution previously noted. The Keys chapter is the best yet on the measurement of fat, while Dublin (using a rather small sample for a life insurance actuarian) cites evidence to show that fat people who lose weight live longer. — S. M. Garn.

Shovel Shaped Incisors.— The upper incisors of all individuals were carefully examined, and in 25 cases a shovel-shaped concavity on the ventral surface could clearly be recognized. The absence of this trait was affirmed in 17 cases, while in 25 individuals dental decay was so advanced that no diagnosis on the occurrence of shovel-shaped incisors was possible.— Emilio Willems. Buzios Island. A Caicara Community in Southern Brazil. Monographs of the American Ethnological Society, XX, 1952, p. 23.

THE RELATIVE THICKNESS OF THE LONG BONES AND THE VERTEBRAE IN PRIMATES[1]

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TWO FIGURES

INTRODUCTION

The thickness of the bones supporting the body represents primarily a problem in mechanics: it must be determined principally by the load the bones have to carry, which is also correlated with the muscular pull exerted on the bone. Hence the thickness of bone should be studied in its relation to body weight or size and, in addition, to the relative, rather than merely the absolute, length of the bone. So far the data of physical anthropology pertaining to the relative thickness of bones, other than cranial ones, are of a purely morphological and descriptive nature and usually limited to the relations between circumference and length of the long limb bones. From such data alone no analysis has been possible of the main factors influencing bone thickness. The writer had long ago suspected that an increase in the length of limb bones is not followed by a corresponding increase in bone thickness. For instance, the percentage relation between the circumference of the shaft and the length of the humerus (="Längendicken-Index" of Martin) has, among adult men, its lowest average (18.2) in the long-limbed Masai (Martin, '28) and its highest (22.1) in the short-limbed Japanese (Nishizuka, '26). If relative limb length does have a bearing on the relation between the thickness and the length of limb bones, this should be studied not only in man but also in all primates, which provide

[1] Brief reports on this study were presented by the author at the International Congress of Anthropology and Ethnology in Vienna, Sept. 4, 1952, and at the meeting of the Swiss Society of Anatomists in Berne, Sept. 18, 1952.

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infinitely greater differences in the proportionate length of their limbs. Likewise a possible influence of body size on relative bone thickness can naturally be analyzed far more advantageously by comparisons between all primates than by those between different groups of man alone. It is the purpose of this paper to provide comparative data for all major groups of primates on the thickness of the long bones of the limbs not only in relation to the length of the same bones, but also in correlation with total limb length and in relation to body size. On the basis of these data it will be shown that isolated information on the length-thickness index of a bone has a very limited meaning since it is largely dependent on several factors of general body build. Naturally there must be still other factors influencing the "bone thickness" which, in this preliminary study, is determined merely by the middle circumference of the bone. The exact thickness and density of the wall of the hollow limb bones and their detailed variations in shape should also be taken into consideration, but this has not yet been undertaken.

This paper deals also with the thickness of the vertebral column at two places, selected as representative, in its relation to general body size. For this particular study the writer could find no relevant previous information in the literature.

As all comparative studies on primates undertaken by anthropologists, this one aims to find any possible specializations of recent man. It is hoped that it will prove useful also in the analysis of fossil remains of primates.

MATERIAL AND TECHNIQUE

The measurements for this study have originated exclusively in the writer's extensive systematic catalogue of skeletal data on primates, assembled during many years. The printed 4-page catalogue records, one for each skeleton, include routine entries for (1) the lengths of humerus, radius, femur, and tibia, (2) the middle circumferences of the shafts of all 6 long limb bones, (3) the transverse diameters of the middle thoracic and lumbar vertebrae, and (4), whenever the body could be meas-

ured before preparation of the skeleton, the anterior trunk height and the body weight besides, of course, the age according to the dentition, the sex, and notes on possible abnormalities of bone. A total of 354 specimens have been selected for the present purpose as to all appearance normal and either fully adult (326) or else very young (28), fluctuating in age between late fetal and early infantile stages. The trunk height is known for only 279 of these specimens. The detailed numerical distribution of this material according to genus, sex and age is apparent from tables 1, 8, 12 and 13. It should be mentioned here also that the bones of the fetal and early infantile specimens have been permanently stored wet to prevent any shrinkage in cartilage and bone. In some of the genera [2] more than one species have been included but space forbids the separate listing of these. It must suffice to mention that no two species of very different body size were used here in one and the same genus. Of the larger series, that for *Macaca* is composed entirely of the species *M. mulatta,* and that for *Hylobates* of the species *H. lar.* In the genera *Nasalis, Symphalangus, Pongo, Pan, Gorilla,* and *Homo* there exists only one real recent species in each. The large majority of these specimens were obtained on the writer's expeditions of former years or have in various other ways been added to his collection. Comparatively few of the specimens used here, and chiefly those without known trunk height, could be studied in the many different museums already referred to in previous publications by the writer. The series for adult man consists of 10 ♀ and 11 ♂ Negroes, 5 Whites, 1 Chinese, 1 Indian, 1 Hawaiian, and 1 Filipino from the Anatomy department of the Johns Hopkins University, and of 2 more ♀ Indians without known trunk height. This is, therefore, deliberately as mixed a series as are probably the series of gorillas, macaques, etc., all of which also include different local races. In addition to measurements on all this material it has been possible to include data on the remarkably thick limb bones and some verte-

[2] These genera, including here more than one species, are: Tarsius, Seniocebus, Cebus, Alouatta, Lagothrix, Papio, Cercopithecus, Erythrocebus, and Pygathrix.

brae of the giant subfossil prosimian *Megaladapis edwardsi*. The latter measurements have been obtained by the writer on perfect casts kindly supplied by the Naturhistorische Museum of Vienna which possesses a splendid, large collection of original bones of this primate. The available casts are all from animals certainly adult; with the exception of the ulna and tibia they were associated with a skull, most likely that of a male (max. length of skull = 293 mm), and ulna and tibia correspond in size perfectly to the radius and fibula respectively.

Bone thickness is here simply represented by the circumference at the (measured) middle of the long bone, in the case of the ulna the coronoid process serves as the proximal end from which "the middle" is to be determined and in the case of the femur the length is measured from the great trochanter. These circumferences have been measured invariably with dental floss, of which one end is re-cut frequently at right angles to the unstretchable waxed thread and the other end of the measured distance is held with sharply pointed forceps with which the floss is transferred to a metal ruler, graduated to half millimeters. In the case of bones with circumferences of less than about 15 mm the thread has been wrapped around twice but, naturally, only half the resulting measure has been recorded. Repeated tests have shown that by this only slightly more laborious procedure the results become more constant than with the use of a single thread, no matter how carefully it is applied. As a technically simple and uniform, yet perhaps somewhat crude, measure for the thickness of the vertebrae the smallest transverse diameter of the vertebral body at its approximate middle has been chosen. For larger and medium-sized vertebrae the sharp ends of Martin's sliding compass are adequate, but for the small vertebrae of many prosimians or Hapalidae an ordinary draftsman-compass with needle-points is greatly preferable. Only the "middle" vertebrae of the thoracic and the lumbar regions have been chosen and in regions with even numbers of vertebrae, the one below the middle was measured; e.g. in thoracic regions with 12 vertebrae the 7th was selected.

The circumferences of the limb bones are usually expressed in relation to the lengths of the corresponding bones. In his primate catalogue the writer has not recorded the lengths of ulna and of fibula, chiefly because their main functional lengths equal those of the adjoining bones, radius and tibia respectively. For this reason the lengths of only 4 limb bones are employed here, those for the humerus, radius and tibia representing greatest lengths, and that for the femur the length from the great trochanter, as has been fully described and illustrated in a former paper by the author ('37). Thus the circumference of the ulna is here expressed in percentage of the length of the radius and the circumference of the fibula in percentage of the length of the tibia. That this particular procedure differs in its results very little from the usual and orthodox one is indicated by the following example: the middle circumference of the fibula in percentage of its greatest length averages, according to Sprecher ('32), 11.9 in 11 adult ♂ Negroes and 12.4 in 17 adult ♂ Whites (Tirol), whereas by expressing the middle circumference of the fibula in percentage of the greatest length of the *tibia* the author obtained averages of 11.8 for his 11 adult ♂ Negroes and 12.8 for his 5 adult ♂ Whites.

In order to study the influence of body size on bone thickness the middle circumferences of the limb bones were also calculated in their relation to the trunk height (suprasternale to symphysion), as the measurement best representing the size of the trunk, the main bodily part supported by the limbs. The vertebral diameters have also been calculated in percentage of trunk height, as best suited for these comparisons.

The following *abbreviations* are used in all the tables and some in the text: Humerus = Hu, Radius = Ra, Ulna = Ul, Femur = Fe, Tibia = Ti, Fibula = Fi, thoracic = thor, lumbar = lumb, the percentage relations between long bone circumferences and lengths of bones = girth-length indices, those between long bone circumferences and trunk height = girth-trunk indices, and the vertebral diameters, expressed in percentage of trunk height = vertebra-trunk indices.

The thickness of long bones in relation to bone length and to limb length

The averages of the girth-length indices for all 6 long limb bones of adult primates are listed in table 1. As pointed out above, the information gained from these data alone is limited to descriptive features. It is seen first of all that the values of man all fall well within the ranges of the corresponding values among the non-human primates. There exist some surprisingly great differences in the relative thickness of these bones in different genera. The humerus, e.g., has an index of 31.9 in *Tana,* but o fonly 12.9 in ♀ *Symphalangus,* and the index for the fibula averages 15.5 in ♂ gorillas, but amounts to only 2.7 in a ♂ *Tarsius* and to 5.0 in a ♂ *Tupaia.* The great apes and man are distinguished as one group by possessing the relatively thickest fibulas. Another unexpected finding consists in the fact that the radius of *Gorilla* is less stout than that of

TABLE 1

Averages of the girth-length indices for a total of 326 adult primates

GENUS	SEX	SPECIMENS	HU	RA	UL	FE	TI	FI
Tupaia	♀	1	25.5	20.0	22.0	22.9	17.8	5.5
	♂	1	25.0	19.6	22.0	22.9	17.9	5.0
Tana	♂	1	31.9	18.2	18.8	25.5	22.3	4.4
Lemur	♀	1	20.9	13.8	14.4	16.8	16.8	8.1
	♂	1	24.7	14.1	15.3	18.0	17.4	9.1
Microcebus	♀	1	26.1	17.6	18.8	19.4	16.2	7.6
	♂	1	27.8	18.3	19.6	19.7	15.9	7.5
Propithecus	♀	1	22.4	13.6	12.6	15.6	15.2	7.0
	♂	1	24.2	14.6	12.6	15.9	15.1	6.3
Daubentonia	♀	1	25.0	18.2	15.3	17.3	16.0	8.2
Nycticebus	♀	1	22.7	15.9	15.2	20.8	15.5	9.2
	♂	1	22.7	16.5	15.2	20.4	16.9	10.7
Perodicticus	♀	1	26.0	17.1	13.7	21.3	15.9	8.8
	♂	1	26.4	18.9	15.3	21.3	17.1	10.1
Galago	♂	1	31.4	20.8	21.7	21.7	19.8	9.3
Tarsius	♀	1	23.4	14.7	13.6	16.1	15.2	3.2
	♂	1	26.6	15.8	13.7	15.7	14.6	2.7

TABLE 1 *(continued)*

GENUS	SEX	SPECIMENS	HU	RA	UL	FE	TI	FI
Seniocebus	♀	1	21.7	16.5	17.6	18.3	16.1	8.1
	♂	1	21.6	14.6	15.8	17.3	15.5	8.6
Oedipomidas	♀	4	23.5	18.3	19.4	19.5	17.9	9.3
	♂	6	23.9	18.6	20.0	19.2	18.0	9.3
Aotus	♀	4	20.8	15.3	16.3	18.4	16.6	8.6
	♂	3	21.0	15.4	16.2	19.3	17.1	8.0
Saimiri	♀	2	20.2	15.6	16.4	18.0	16.7	8.0
	♂	8	21.5	15.9	16.3	18.3	17.0	8.3
Cebus	♀	5	21.2	15.2	16.3	18.1	17.2	8.4
	♂	11	22.6	15.8	17.3	19.0	18.8	9.0
Alouatta	♂	5	21.9	15.6	16.0	21.9	20.3	10.1
Lagothrix	♀	1	17.5	12.0	12.7	18.6	17.0	8.2
	♂	1	18.5	12.3	13.0	19.7	18.7	8.7
Ateles	♀	5	17.0	10.3	10.9	20.2	18.4	8.4
	♂	4	17.5	12.2	11.9	21.2	19.5	9.1
Macaca	♀	12	23.3	17.4	16.2	21.6	21.7	10.8
	♂	12	25.9	18.8	17.7	23.6	23.2	11.0
Papio	♀	4	24.0	16.3	15.3	22.1	22.9	10.4
	♂	4	25.5	17.2	14.7	22.2	21.9	10.1
Cercocebus	♀	5	22.9	16.2	14.9	20.5	18.9	8.9
	♂	1	23.1	17.6	15.7	20.7	22.2	9.9
Cercopithecus	♀	5	22.9	18.6	15.5	21.1	20.4	9.7
	♂	8	25.0	17.9	16.7	21.3	19.8	9.9
Erythrocebus	♀	2	22.8	16.2	12.8	20.9	20.4	10.0
Pygathrix	♀	2	22.0	15.8	15.2	19.4	21.3	9.5
	♂	4	21.7	14.7	14.1	18.6	19.6	9.0
Nasalis	♀	15	18.7	12.6	11.6	18.8	19.1	8.6
	♂	10	20.0	13.6	12.9	19.6	20.4	9.5
Hylobates	♀	24	13.4	8.4	8.5	15.7	16.7	9.1
	♂	24	13.6	8.7	8.8	15.8	16.9	9.3
Symphalangus	♀	3	12.9	7.6	8.7	17.1	18.1	11.3
	♂	7	14.0	8.5	9.5	18.6	18.5	10.9
Pongo	♀	12	19.4	11.9	13.5	24.3	21.4	11.5
	♂	12	19.9	13.0	14.7	25.1	22.7	12.4
Pan	♀	14	25.0	17.1	17.3	25.5	24.7	14.0
	♂	12	25.7	17.4	17.6	25.7	25.7	14.4
Gorilla	♀	12	22.5	17.0	18.8	29.6	26.0	14.2
	♂	12	25.6	18.4	21.0	31.7	29.8	15.5
Homo	♀	12	21.1	17.3	18.4	20.3	22.2	11.4
	♂	20	21.6	18.6	20.3	20.5	22.8	12.2

man,[3] whereas the reversed relation exists in regard to the other bones, especially those of the lower limb. Among higher primates the radius is relatively thickest in man, though the African apes stand very close in this respect and among lower primates there are a number of forms with radii as thick or even thicker than in man. In all higher primates and in all New World monkeys the ulna is invariably thicker than the radius in the middle of the forearm, but in all Old World monkeys the reversed relation has been found without exception and the prosimians are quite variable in this respect. It is of interest also to note that in these girth-length indices the tibia surpasses the femur in man, gibbon and some of the lower catarrhines, but not in any of all the other recent primates. Surpassing all the girth-length indices in table 1 are those of the extinct prosimian *Megaladapis* which were determined as follows: Hu 37.8, Ra 23.4, Ul 30.6, Fe 38.7, Ti 39.7, Fi 27.3. All these values demonstrate clearly the exceptional thickness of the limb bones of this giant primate, evident also from the examples shown in figure 1.

From the figures in table 1 it is seen that in general males possess relatively thicker limb bones than females. The apparent exceptions to this rule occur chiefly in the genera in which one or both sexes are represented by only one or two specimens or by more than one species. This sex difference, well-known for man,[4] is particularly marked in such species as the gorilla, the proboscis monkey and the macaque, in which the two sexes differ greatly in body size, and less pronounced

[3] This is supported by the data of Fischer ('06) for the length-thickness index of the radius, which he found to average 17.1 in 5 gorillas, compared with 18.1 in 25 Germans and even 20.2 in 3 Japanese. Since these figures are based upon the *smallest*, instead of the middle, circumference of the radius, they are not directly comparable to those in table 1. Also, Fischer's small series of non-human primates are not segregated according to age and sex.

[4] This sex difference in relative thickness of limb bones has been demonstrated, e.g., by Hrdlička ('32 and '38) in exceptionally large series of human humeri and femora, using diameters of the shaft, instead of circumferences. It seems to be doubtful, however, that in this material sex was actually *known* in more than part of the cases.

TABLE 2

Ranges of variations of the girth-length indices for the larger series of single species

SPECIES	SEX	SPECIMENS	HU	RA	UL	FE	TI	FI	AVERAGE RANGE
Macaca mulatta	♀	12	21.6–25.2	16.0–20.8	12.4–19.1	19.3–23.3	20.3–23.7	8.5–13.7	4.6
	♂	12	23.4–28.2	17.1–22.0	15.8–20.9	21.7–26.8	22.3–24.3	9.6–13.0	4.2
Nasalis larvatus	♀	15	17.3–20.3	11.5–13.4	10.2–12.2	17.4–19.6	17.7–20.6	6.8–10.1	2.5
	♂	10	19.2–21.4	12.9–14.4	12.0–14.0	18.5–20.6	18.7–21.7	8.7–10.2	2.1
Hylobates lar	♀	24	12.3–14.9	7.4–9.3	7.4–9.3	14.1–17.4	15.2–18.4	7.1–10.1	2.6
	♂	24	11.7–15.5	7.5–10.0	7.2–10.0	14.3–17.5	14.9–18.7	8.2–10.4	3.1
Pongo pygmaeus	♀	12	16.0–22.1	10.1–13.3	12.5–14.6	21.2–27.1	18.7–23.0	10.0–13.8	4.2
	♂	12	16.9–24.2	11.3–14.9	13.3–16.7	21.4–30.5	19.6–27.0	10.8–14.8	5.8
Pan satyrus	♀	14	22.4–28.0	14.4–20.1	15.2–20.9	22.7–27.5	22.9–28.6	12.5–16.1	5.2
	♂	12	21.7–28.4	14.9–19.4	15.6–20.8	21.3–29.2	21.1–30.1	12.6–16.4	6.2
Gorilla gorilla	♀	12	20.9–26.4	15.2–17.9	17.6–20.8	27.5–31.9	23.2–28.9	12.5–15.7	4.1
	♂	12	22.1–30.2	16.4–22.3	18.7–23.4	28.7–36.0	25.8–34.4	12.7–21.0	7.2
Homo sapiens	♀	12	18.2–22.7	15.3–19.8	15.7–22.2	18.0–22.8	20.4–25.7	9.7–13.2	4.8
	♂	20	19.2–24.3	17.3–23.0	17.4–23.7	18.5–21.7	20.8–26.4	10.0–15.9	5.3

in species, such as the chimpanzee and gibbon, whose females are but little smaller than males.

The ranges of individual variations in these girth-length indices are shown in table 2 for the larger series of single species. In the last column of the table are listed the arithmetic means of the differences between the maxima and minima, as tabulated in the other columns. From these "average ranges" it can be seen most conveniently that these indices vary no more in man than in at least the great apes, even though the human series is composed of several races. If the size of the indices themselves is taken into consideration in comparing these average ranges the gibbons would no longer appear to be quite so uniform in contrast to, e.g., gorillas with their far higher indices. It is of interest also to note from these data that relative bone thickness is considerably more variable in males than in females in anthropoids and in man, but not in the monkeys of table 2.

From a study of the data in table 1 it can be seen that extremely low indices occur in the primates whose upper or lower limbs have become notoriously lengthened. For instance, the lowest indices among prosimians belong to the lower limbs of *Tarsius*, which are distinguished by their great proportionate length; the lowest indices among platyrrhines exist in the arm bones of *Ateles*, known for its spider-like long upper limbs; and among the higher primates the Hylobatidae possess not only the minimal indices for the arm bones, but also the maximal increase in relative arm length of all primates. This relation between relative bone thickness and *relative* bone length is more fully demonstrated in table 3, which compares the actual relative limb lengths with the averages of the three girth-length indices of the corresponding limbs. These averages have been calculated merely for the sake of condensation in order to express with only one figure the degree of bone thickness in the upper or the lower limbs of a particular primate genus. From table 3 it is evident that not only the above mentioned long-limbed forms — tarsier, spider monkey and gibbon — have extreme girth-length indices, but that, generally

speaking, these girth-length indices stand in inverse relation to the relative lengths of the limbs. This rule has many more or less pronounced exceptions (largely due to the influence of body size, discussed below), but the trend is unmistakable in each of the 4 groups of genera and for both the upper and the lower limb: that the shorter a limb in proportion to the trunk the relatively thicker are its bones and vice versa. For instance, among the prosimians the shortest relative upper limb

TABLE 3

Comparisons between relative limb length and average relative bone thickness in four systematic groups of primates, on the left for upper limb and on the right for lower limb. A = Hu + Ra lengths in per cent of trunk height arranged according to increasing size, B = averages of girth-length indices for Hu, Ra and Ul as listed in table 1, C = Fe + Ti lengths in per cent of trunk height arranged according to increasing size, D = averages of girth-length indices for Fe, Ti and Fi as listed in table 1. All averages for both sexes combined.

GENUS	A	B	GENUS	C	D
Tana	55.8	23.0	Tupaia	77.3	15.3
Tupaia	56.4	22.4	Tana	78.5	17.4
Microcebus	57.2	21.4	Microcebus	79.2	14.4
Lemur	67.5	17.2	Perodicticus	82.1	15.8
Galago	70.8	24.6	Nycticebus	85.4	15.6
Perodicticus	71.6	19.6	Lemur	95.9	14.4
Nycticebus	73.9	18.0	Galago	106.0	16.9
Propithecus	79.9	16.7	Daubentonia	129.0	13.8
Daubentonia	91.2	19.5	Propithecus	137.3	12.5
Tarsius	92.6	17.9	Tarsius	170.0	10.6
Oedipomidas	64.3	20.6	Oedipomidas	86.2	15.5
Aotus	70.4	17.5	Saimiri	92.4	14.4
Saimiri	72.0	17.7	Aotus	94.0	14.7
Seniocebus	74.9	18.0	Seniocebus	101.3	14.0
Cebus	88.0	18.1	Alouatta	102.6	17.4
Alouatta	105.6	17.8	Cebus	110.0	15.1
Lagothrix	115.0	14.3	Lagothrix	117.1	15.2
Ateles	127.7	13.3	Ateles	118.6	16.1
Cercopithecus	75.6	19.4	Cercopithecus	89.5	17.0
Cercocebus	81.3	18.4	Macaca	94.7	18.7
Pygathrix	82.5	17.3	Erythrocebus	96.8	17.1
Macaca	83.1	19.9	Cercocebus	99.0	17.0
Erythrocebus	88.8	17.3	Papio	100.9	18.3
Papio	95.2	18.8	Pygathrix	101.0	16.2
Nasalis	98.0	14.9	Nasalis	106.1	16.0
Homo	112.9	19.6	Pongo	102.7	19.6
Pan	113.1	20.0	Gorilla	104.4	24.5
Gorilla	120.6	20.6	Pan	107.3	21.7
Pongo	147.5	15.4	Symphalangus	125.7	15.8
Hylobates	183.9	10.3	Hylobates	139.1	13.9
Symphalangus	187.2	10.2	Homo	159.6	18.2

length (56) is accompanied by an average girth-length index of 23.0, whereas the longest (93) by an index of only 17.9. Among the platyrrhines the minimum relative upper limb length (64) exists in the form with the maximum average girth-length index of 20.6, whereas the minimum of 13.3 in the latter index goes with the maximum relative arm length (128). Among the lower catarrhines that with the shortest arms (76) has an average girth-length index of 19.4 and that with the longest arms (98) one of only 14.9, and among the higher primates the three forms with relative arm lengths of 113 to 121 have average girth-length indices of 19.6 to 20.6, whereas the three other forms with relative arm lengths of 148 to 187 possess corresponding values of only 10.2 to 15.4. In regard to the relative length of the lower limbs the influence on the average girth-length indices appears to be less marked, at least in the groups of New and Old World monkeys which vary comparatively little in lower limb length. Among the prosimians the three genera with the shortest hind legs (77 to 79) have average girth-length indices of 14.4 to 17.4, whereas the three genera with the longest hind legs (129 to 170) have corresponding indices of only 10.6 to 13.8. Among the higher primates, finally, the three great apes with their relative lower limb lengths of 103 to 107 have girth-length indices of 19.6 to 24.5 in contrast to the Hylobatidae which combine much longer lower limbs (126 and 139) with much lower indices of bone thickness (15.8 and 13.9). Man is rather exceptional in this respect, inasmuch as his great relative lower limb length (160) is accompanied by an average girth-length index of 18.2 which, though lower than in the great apes, lies far above the minimal values, found in the Hylobatidae with their shorter legs. That the reasons for this lie partly in the great difference in size between man and gibbons and partly in man's erect posture will be discussed below.

The enormous thickness of the limb bones of *Megaladapis*, discussed above, is the result not only of the huge body size, but partly also of the short relative length of the limbs. For determining the latter in the manner used here, the trunk

height is required which can be obtained approximately from the careful reconstruction of the entire skeleton published by Lorenz von Liburnau ('05), who had enviably rich material at his disposal, and by comparing the lengths of the huge vertebrae of *Megaladapis* with the corresponding measurements in

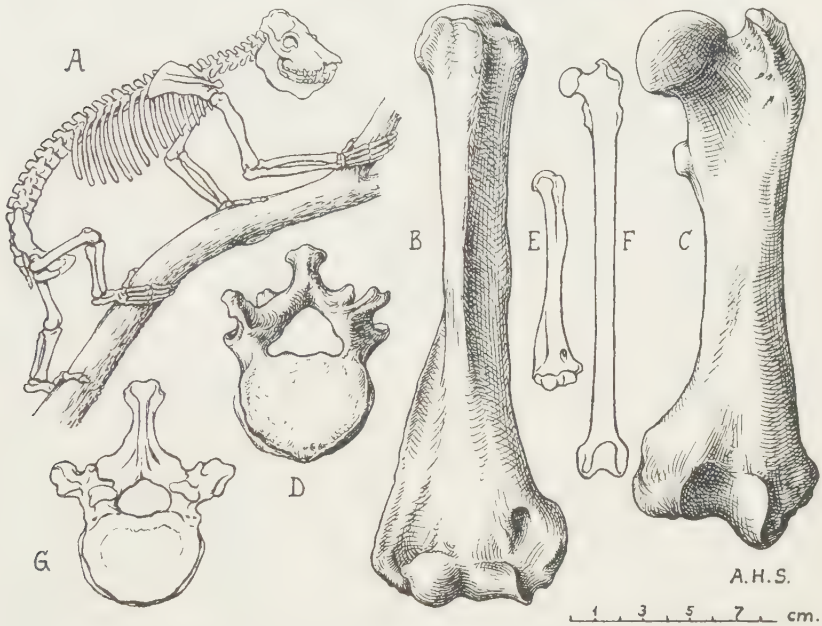

Fig. 1 A = reconstructed skeleton of *Megaladapis edwardsi* after Lorenz von Liburnau ('05); B = right humerus, C = left femur, and D = last or second-last thoracic vertebra of an adult *Megaladapis;* E = right humerus, and F = left femur of an adult male *Propithecus verreauxi;* G = last thoracic vertebra of a large adult male gorilla. B to G all drawn in natural size and here reduced as the scale in lower right corner.

recent lemurs with known trunk heights. On this basis the writer feels confident that the trunk height of an adult *Megaladapis* with spinal column straightened must have measured somewhere between 600 and 650 mm and most likely about 630 mm. With this assumption the relative length of the upper limb of *Megaladapis* would equal 75.1 and that of its lower limb only 61.6. The former value is about an average one for prosimians, whereas the latter is clearly the lowest among all

primates (see table 3, columns A and C). That *Megaladapis* is distinguished by extremely shortened hind limbs is illustrated in figure 1, A and appears also from the fact that its accurately determined intermembral index of 121.7 lies far above corre-

TABLE 4

Comparison between relative limb length and average relative bone thickness in 20 adult men. A = Hu + Ra lengths in per cent of trunk height arranged according to increasing size, B = averages of girth-length indices for Hu, Ra and Ul, C = Fe + Ti lengths in per cent of trunk height arranged according to increasing size, D = averages of girth-length indices for Fe, Ti and Fi, last column = same numbers as in first column.

NO.	RACE	WEIGHT	A	B	C	D	NO.
1	Hawaiian	77	95.4	22.3	134.3	20.1	1
2	White	64	102.2	21.7	141.6	20.3	2
3	White	73	102.5	23.3	143.1	21.1	3
4	Negro	66	105.5	21.1	148.2	18.1	4
5	Chinese	76	105.5	19.6	150.3	18.0	7
6	Indian	82	106.8	19.2	150.5	17.6	5
7	White	63	107.1	18.9	151.7	18.8	6
8	White	80	110.5	19.6	154.3	19.0	10
9	White	69	110.7	18.8	155.5	17.6	9
10	Negro	63	111.4	21.1	156.7	20.7	15
11	Negro	73	113.5	19.7	157.6	17.8	8
12	Negro	77	114.7	19.8	163.0	18.1	11
13	Negro	72	115.0	20.5	165.0	17.3	14
14	Negro	67	115.1	20.0	165.2	17.6	13
15	Negro	87	115.2	21.0	170.1	16.8	12
16	Filipino	74	121.4	18.2	171.5	17.5	19
17	Negro	55	122.5	19.3	174.0	18.2	17
18	Negro	73	123.7	20.5	174.3	16.7	16
19	Negro	67	127.8	19.2	176.7	18.6	18
20	Negro	65	128.1	19.2	177.2	17.3	20
	Average	71.1	112.7	20.1	159.0	18.4	

sponding indices in all other prosimians, being surpassed by only orang, gibbon and siamang (see table 6). In the latter three extreme brachiators the intermembral indices are exceptionally high in consequence of their enormous relative upper limb lengths, whereas in *Megaladapis* the index has increased so much as a result of an extreme shortening of the

lower limb length. This shortening has affected the lengths but not the girths of the bones, so their girth-length indices have risen to an average value for the three lower limb bones of 35.2 which is more than twice the highest value among other prosimians. Since the relative length of the upper limb of *Megaladapis* (ca. 75) has remained about average, the mean girth-length index of the upper limb bones of 30.6 has risen above the maximum corresponding value among other prosimians (24.6 for *Galago* with relative arm length of 71) by only an amount expected as the result of the great difference in body size.

That, even intraspecifically, individuals with long limbs tend to have more slender limb bones than those with short limbs is shown by the example of 20 adult men in table 4. These are listed according to increasing relative limb lengths. In the first 10 with the shortest limbs the average of the indices for relative bone thickness equals 20.6 for the upper limb bones and 19.1 for the lower ones, but in the second 10 men, with longer limbs, both corresponding values are lower, namely 19.7 and 17.6 respectively. In contrast to this the body weight does not seem to influence the girth-length indices to a great extent within the same species, sex and age. At least in the 10 men with the lightest body weights the average of the indices for the thickness of the leg bones (column D) amounts to 18.1 and in the 10 heavier men to 18.6. In considering only extremes in weight its influence appears to be more significant. For instance, in the lightest Negro (55 kg) the average girth-length index for the upper limb bones equals 19.3 and that for the lower ones 18.2, but in the heaviest Negro (87 kg) the corresponding figures are 21.0 and 20.7 (see also table 5).

The findings presented so far have demonstrated that an evolutionary increase in limb length is no reason for an increase in relative thickness of limb bones, which retain their circumference with little if any change. Slender limb bones, therefore, merely indicate great relative limb length and vice versa, provided the bones compared are from specimens of reasonably similar body size. This rule pertains not only to

primates, but to other mammals as well, as shown most convincingly by different breeds of domestic dogs, including achondroplastic hounds. Stockard ('41), e.g., has illustrated the limb skeletons of many long-limbed and of extremely short-limbed dogs, and it is readily seen from his beautiful photographs that the thickness of the limb bones remains practically unaltered by their enormous changes in length. Human racial differences in the girth-length indices of long bones are also primarily due to differences in relative limb lengths and the frequent claim that the specially thick limb bones of the Neanderthaler (La Chapelle) speak for enormous muscular strength more probably indicates comparatively short limbs.

TABLE 5

The girth-length indices of a very large male rhesus macaque and of a small adult male Philippine macaque

	HU	RA	UL	FE	TI	FI	AVERAGE
Macaca mulatta	25.4	19.0	16.7	23.1	23.5	11.2	19.8
Macaca philippinensis	19.2	13.3	12.5	18.7	18.2	7.9	15.0

That the girth-length indices are also influenced by body size or weight has been shown above by examples from one and the same species with rather small differences in size. Much larger size differences can occur in related species and then do affect the girth-length indices to a marked extent, as shown by the figures in table 5. Of the two macaques compared in this small table the rhesus is an exceptionally large male with a body weight of 18.14 kg and a trunk height of 415 mm, whereas the Philippine monkey is, though fully adult, the smallest male in the writer's collection of these animals, having a body weight of only 3.5 kg and a trunk height of 234 mm. The relative lengths of the limbs are practically alike in both these specimens, but all the girth-length indices are larger in the one which is more than 5 times heavier than in the other one.

Is the *absolute* thickness of the long bones influenced by the proportionate length of the limbs? This problem can be attacked with the complete elimination of the factor of body size

by comparing the percentage relations between the sum of the circumferences of the upper limb bones and that of the lower ones with the intermembral indices which give the length of the upper limb in percentage of that of the lower one (without distal segments). This is done in table 6 in which the 31 genera are listed according to increasing intermembral indices. In 22

TABLE 6

Comparisons between the averages of (A) the intermembral index (= Hu + Ra lengths in per cent of Fe + Ti lengths) and (B) the sum of the circumferences of the three bones of the upper limb in per cent of the sum of the circumferences of the three bones of the lower limb.

GENUS	A	B	GENUS	A	B
Tarsius	54.5	87.6	Cercopithecus	84.4	94.7
Propithecus	58.1	78.8	Nycticebus	86.6	100.6
Galago	66.9	97.8	Perodicticus	87.2	108.5
Lemur	70.4	85.0	Macaca	87.7	93.3
Homo	70.6	74.6	Erythrocebus	91.7	93.2
Daubentonia	70.7	100.0	Nasalis	92.4	87.3
Tana	71.1	93.5	Papio	94.3	99.5
Microcebus	72.3	107.7	Lagothrix	98.2	92.8
Tupaia	73.0	105.1	Alouatta	103.0	106.5
Seniocebus	73.8	93.9	Pan	105.3	99.7
Oedipomidas	74.6	98.1	Ateles	108.1	87.9
Aotus	74.9	89.7	Gorilla	115.5	97.2
Saimiri	77.9	94.3	Hylobates	132.2	98.8
Cebus	80.1	96.8	Pongo	143.6	114.2
Pygathrix	81.6	88.5	Symphalangus	148.9	98.6
Cercocebus	82.3	90.2			

of these genera the percentage relations between the circumferences of the bones of the upper and of the lower limb vary between 90 and 110, i.e. the bones of both limbs have roughly the same absolute thickness, if all are considered in this generalization. The intermembral indices vary in these 22 genera between 67 and 149. It appears, therefore, that the absolute thickness of the limb bones can remain practically unchanged with enormous changes in the relation in length between upper and lower limbs. Even in *Tarsius*, which has the lowest of all intermembral indices, the circumferences of the upper limb

bones equal 88% of those of the enormously lengthened lower limb bones. The outstanding exceptions to this finding are the extremes in column B of table 6, namely the maximum of over 114 in orang-utan and the minimum of 74.6 in man. The former has, according to these figures, very thick upper limb bones in comparison with the lower ones and the latter very thick lower limb bones in contrast to the upper ones; furthermore, the former has the second highest intermembral index and the latter one of the lowest ones. *Propithecus* with an intermembral index even lower than in man also has a very low bone thickness index (79). These extremes in the relation between the thickness of the upper and of the lower limb bones are not simply due to the great increase in the length of the orang's arms or of man's legs, but are probably connected in some way with the specialized bimanual or bipedal locomotion in these primates.

The thickness of long bones in relation to the size of the trunk and the entire body

If the circumference of long limb bones is studied in relation to some measurement representing the size of the trunk, which is the main load carried by the limbs, we obtain a method, though admittedly crude, for answering the question of a possible influence of body size on the thickness of bones serving primarily as supports. The data in table 7 show that, in relation to trunk height, the girths of all the long bones are significantly smaller in a Philippine macaque than in a rhesus macaque which is over 5 times heavier. That this result might have been expected becomes evident from the following simple theoretical considerations: if a trunk were cube-shaped, weighing 1 kg and measuring 10 cm along each side, and could be supported by one square rod 1 cm in width, then a 100 times larger cube of the same material (= 100 kg) would measure 46.4 cm in each dimension and could be supported by 100 equal square rods, when bunched having a width of 10 cm and a perimeter of 40 cm. In the first instance the percentage rela-

tion between girth of support (4 cm) and diameter of load (="trunk height") (10 cm) equals 40, whereas in the second and 100 times heavier example the girth of the support (40 cm) in percentage of the diameter of the load (46.4 cm) has increased more than two times, namely to 86. Theoretically,

TABLE 7

The girth-trunk indices of the adult male rhesus macaque of 18.1 kg and of the adult male Philippine macaque of 3.5 kg, used also in table 5

	HU	RA	UL	FE	TI	FI	AVERAGE
Macaca mulatta	10.4	8.0	7.0	11.1	10.6	5.1	8.7
Macaca philippinensis	10.0	6.8	6.4	10.7	9.8	4.3	8.0

therefore, a hundredfold increase in "body" weight should increase the girth-trunk indices 2.15 times, but a fivefold increase in weight, as calculated in a corresponding manner, only 1.3 times (from 40 to 52 on the basis of the above arbitrarily chosen units). Actually the fivefold gain in body weight in the heavier of the two macaques of table 7 has increased the average girth-trunk index only 1.1 times, a value in reasonably close agreement with the theoretical expectation, if it is considered that actual trunk height and the above theoretical one, as well as actual body weight (including the limbs) and the theoretical cube-shaped load are, naturally, comparable to only a limited degree.

The enormous differences in body size which occur among recent primates provide an excellent basis for further study of the influence of "load" on relative bone thickness. The average percentage relations between the middle circumferences of all the long bones and the trunk height in 31 genera of primates are listed in table 8. It is seen at once that these girth-trunk indices can differ extensively in some of the genera. For instance, the index for the humerus is only 7.1 in a female *Microcebus,* whereas it is 18.2 in male gorillas and the difference between the indices for the femur in these same forms, which are the smallest and the largest of all recent primates, is even more marked. The influence of body size upon these

TABLE 8

Averages of the girth-trunk indices for a total of 251 adult primates

GENUS	SEX	SPECIMENS	HU	RA	UL	FE	TI	FI
Tupaia	♀	1	7.5	5.4	5.9	8.6	7.0	2.2
	♂	1	7.4	5.2	5.9	8.5	7.2	2.0
Tana	♂	1	9.1	5.0	5.1	9.9	8.8	1.7
Lemur	♀	1	7.1	4.7	4.9	8.2	7.8	3.7
	♂	1	8.1	4.9	5.3	8.9	8.1	4.3
Microcebus	♀	1	7.1	5.2	5.6	7.1	6.5	3.1
	♂	1	7.5	5.5	5.9	7.6	6.7	3.2
Propithecus	♀	1	8.4	5.5	5.1	11.4	9.4	4.3
	♂	1	9.6	6.2	5.3	11.9	9.8	4.0
Daubentonia	♀	1	11.4	8.3	7.0	11.4	10.1	5.2
Nycticebus	♀	1	8.5	6.0	5.7	9.1	6.5	3.9
	♂	1	8.2	6.1	5.6	8.9	7.0	4.4
Perodicticus	♀	1	9.3	6.1	4.9	9.0	6.4	3.6
	♂	1	9.3	6.9	5.6	8.8	6.8	4.0
Galago	♂	1	11.0	7.4	7.7	11.9	10.1	4.8
Tarsius	♀	1	10.0	7.8	7.2	13.5	12.5	2.6
	♂	1	10.5	7.9	6.8	13.4	12.9	2.4
Seniocebus	♀	1	8.2	5.7	6.1	9.0	8.2	4.1
	♂	1	8.6	5.5	5.9	8.6	8.2	4.5
Oedipomidas	♀	3	8.2	5.8	6.0	8.6	8.1	4.1
	♂	3	8.2	5.6	6.1	8.0	7.8	4.1
Aotus	♀	2	7.7	5.1	5.5	8.8	8.1	4.2
	♂	2	7.1	5.1	5.4	8.4	7.7	3.6
Saimiri	♀	1	7.2	5.5	5.8	8.7	7.8	3.7
	♂	5	8.2	5.7	5.8	8.5	7.9	3.9
Cebus	♀	4	9.8	6.2	6.8	10.1	9.0	4.5
	♂	10	10.1	6.8	7.4	10.5	9.8	4.7

TABLE 8 *(continued)*

GENUS	SEX	SPECIMENS	HU	RA	UL	FE	TI	FI
Alouatta	♂	3	11.6	7.9	8.0	11.3	9.6	4.9
Lagothrix	♀	1	10.5	6.6	7.0	11.3	9.8	4.7
	♂	1	10.9	6.8	7.2	11.7	10.5	4.9
Ateles	♀	5	11.4	7.3	7.7	13.6	11.7	5.3
	♂	2	10.8	7.6	7.6	12.9	11.2	5.4
Macaca	♀	12	9.8	7.2	6.7	10.8	9.9	4.9
	♂	12	10.9	7.9	7.4	11.9	10.7	5.1
Papio	♀	3	11.3	8.2	7.8	12.1	11.1	5.0
	♂	1	11.7	10.0	8.1	12.5	11.5	5.1
Cercocebus	♀	4	8.8	6.6	6.2	10.3	8.8	4.3
	♂	1	10.1	7.6	6.8	11.7	11.2	4.9
Cercopithecus	♀	3	8.9	7.2	5.9	9.9	9.3	4.5
	♂	7	9.7	7.0	6.5	10.1	9.2	4.6
Erythrocebus	♀	2	9.7	7.4	5.9	10.2	9.7	4.7
Pygathrix	♀	2	9.3	6.5	6.2	10.5	10.2	4.6
	♂	3	8.5	6.0	5.7	9.9	9.4	4.2
Nasalis	♀	15	8.7	5.9	5.5	10.0	9.1	4.1
	♂	10	9.6	6.7	6.3	10.8	10.1	4.7
Hylobates	♀	24	11.4	7.8	7.9	11.5	10.5	5.7
	♂	24	11.9	8.3	8.4	11.8	10.9	6.0
Symphalangus	♂	3	12.0	8.1	9.0	12.1	10.6	6.1
Pongo	♀	5	14.1	8.7	9.7	13.2	10.4	5.8
	♂	2	15.2	9.8	11.1	14.4	11.2	6.3
Pan	♀	14	15.3	9.7	9.8	15.5	12.6	7.1
	♂	6	16.4	9.8	10.2	15.5	13.2	7.3
Gorilla	♀	3	16.7	9.9	10.8	17.9	13.2	6.9
	♂	4	18.2	10.0	11.6	18.7	13.9	6.9
Homo	♀	10	12.9	8.2	8.7	16.9	15.9	7.9
	♂	20	13.7	9.0	9.8	17.4	16.5	8.8

indices will be discussed further after some other conclusions from table 8 have been mentioned. Again it is found that in platyrrhines, anthropoid apes and man the ulna has a larger middle girth than the radius, whereas in all lower catarrhines the reversed relation occurs. Only in the orang-utan and in male chimpanzees is the index for the femur much smaller than that for the humerus; in all the other genera in table 8 these two indices are either very similar or, more often, that for the femur surpasses the one for the humerus to a marked degree, which reaches its extreme in man. In all the primates for which series of male and female individuals could be investigated (*Cebus, Macaca, Nasalis,* the anthropoids, and man) the indices of males are larger than the corresponding ones of females, these differences being specially marked in the forms with great sexual differences in general body size.

Outstandingly high values of these girth-trunk indices exist among lower primates only for the femur and tibia and this in the tarsier, which is extremely specialized for jumping and is the only primate with a vestigial fibula, and in the spider monkey, the only monkey which can run on its hind legs alone with ease. The highest of all indices are found in the great apes and man (regarding the fibula also in the Hylobatidae). Within this group man has the lowest indices for the bones of the upper limb, but the second highest for the femur and the highest of all for tibia and fibula. This extreme thickness of the last two bones, relative to trunk size, represents an unsuspected and clear-cut specialization of man.

The variability of the girth-trunk indices in the larger series of primates investigated is shown in table 9. These ranges of variations are of practically the same magnitude in relation to the average size of the indices as the ranges of the girth-length indices shown in table 2.

For the sake of easy comparability of the general degree of relative bone thickness with the body weight the averages of the 6 girth-trunk indices listed in table 8 are given in table 10 together with the weights. These data leave no doubt that in general the smallest primates of a systematic group have

TABLE 9

Ranges of variations of the girth-trunk indices for the larger series of single species

SPECIES	SEX	SPECIMENS	HU	RA	UL	FE	TI	FI	AVERAGE RANGE
Macaca mulatta	♀	12	9.0–10.8	6.5– 8.3	5.9– 7.6	9.7–11.8	9.4–10.6	3.9– 6.2	1.8
	♂	12	9.9–11.8	7.1– 9.1	6.6– 9.0	10.5–13.5	9.7–11.9	4.5– 6.4	2.2
Nasalis larvatus	♀	15	8.3– 9.8	5.3– 6.7	5.0– 6.1	9.3–11.0	8.5– 9.8	3.4– 4.5	1.3
	♂	10	9.1–10.3	6.4– 7.2	5.9– 6.8	10.2–11.6	9.4–11.1	4.5– 5.2	1.1
Hylobates lar	♀	24	10.4–12.7	7.2– 8.5	6.9– 8.7	10.6–12.6	9.3–11.6	4.7– 6.7	2.0
	♂	24	10.6–14.0	7.5– 9.3	6.8– 9.6	10.2–13.6	9.3– 12.8	5.1– 6.7	2.6
Pan satyrus	♀	14	12.9–18.6	8.4–11.7	8.5–11.6	13.4–17.6	11.0–14.2	6.0– 8.3	3.6
	♂	6	15.4–17.4	8.8–10.6	9.1–10.9	13.6– 17.6	10.6–14.8	6.6– 8.0	2.5
Homo sapiens	♀	10	11.7–13.9	7.6– 8.9	7.8– 9.6	15.8–18.1	14.2–17.3	7.2– 9.0	2.1
	♂	20	11.8–16.0	7.8– 9.9	8.6 10.9	15.4–20.0	15.0–18.4	7.3–11.5	3.5

relatively thinner limb bones than the largest forms. Among prosimians, e.g., the average girth-trunk indices equal 5.9 to 6.6 in *Microcebus, Tupaia* and *Tana* which weigh from 60 to 300 gm, compared with 6.7 to 8.9 in *Galago, Perodicticus, Daubentonia* and *Propithecus* which weigh between 1.1 and 4 kg. Exceptional in this respect is chiefly *Tarsius* which, though very

TABLE 10

The averages of the girth-trunk indices of the primates in table 8 in order of increasing average body weight within the major systematic groups (the Colobinae are here separated from the Cercopithecinae). Only in the genera with very great sex difference in weight and in the genus Homo have the sexes been listed separately.

GENUS	SEX	KG	INDEX	GENUS	SEX	KG	INDEX
Microcebus	♀♂	0.06	5.9	Erythrocebus	♀	4.4	7.9
Tarsius	♀♂	0.12	9.1	Cercopithecus	♀♂	4.5	7.7
Tupaia	♀♂	0.20	6.1	Cercocebus	♀♂	6.2	8.2
Tana	♂	0.30	6.6	Macaca	♀♂	8.9	8.6
Nycticebus	♀♂	1.0	6.7	Papio	♀	20.0	9.3
Galago	♂	1.1	8.8	Papio	♂	32.0	9.8
Perodicticus	♀♂	1.2	6.7				
Daubentonia	♀	1.2	8.9	Nasalis	♀	11.3	7.2
Lemur	♀♂	2.0	6.3	Pygathrix	♀♂	12.8	7.6
Propithecus	♀♂	4.0	7.6	Nasalis	♂	22.0	8.0
Seniocebus	♀♂	0.22	6.9	Hylobates	♀♂	5.6	9.3
Oedipomidas	♀♂	0.53	6.7	Symphalangus	♂	11.1	9.7
Aotus	♀♂	1.0	6.4	Pongo	♀	37.1	10.3
Saimiri	♀♂	1.1	6.6	Pan	♀♂	47.5	11.8
Cebus	♀♂	3.3	8.0	Homo	♀	59.0	11.8
Lagothrix	♀♂	4.8	8.5	Homo	♂	71.1	12.5
Ateles	♀♂	8.0	9.3	Pongo	♂	74.6	11.3
Alouatta	♂	8.1	9.0	Gorilla	♀	80.0	12.6
				Gorilla	♂	166.0	13.2

small, has comparatively thick limb bones. The platyrrhines show the influence of body size on the average size of the girth-trunk indices very clearly, and so do the lower catarrhines, if separated by subfamilies, since the Colobinae are generally distinguished from the Cercopithecinae by relatively thinner limb bones in spite of similar body weights. Among the higher primates the small gibbons possess the smallest average girth-trunk index, the larger siamangs stand second in this respect and the huge male gorillas show the highest index.

As discussed above, the trunk height of *Megaladapis* can be roughly estimated as somewhere near 630 mm. On that basis the girth-trunk indices of this giant prosimian are the following: Hu 15.1, Ra 8.3, Ul 10.8; Fe 14.0, Ti 10.2, Fi 7.0, and the average index is 10.9. The latter average fits in table 10 among the largest primates and greatly surpasses the averages for all other and very much smaller Lemuroidea.

TABLE 11

Comparison between body weights and the averages of the girth-trunk indices for all six limb bones in 20 adult men. The numbers (No.) correspond to those used in table 4

WEIGHT	AVER. INDEX	NO.	WEIGHT	AVER. INDEX	NO.
kg			*kg*		
55	13.5	17	73	12.6	11
63	11.4	7	73	12.8	3
63	12.8	10	73	14.2	18
64	12.3	2	74	12.4	16
65	11.7	20	76	11.8	5
66	12.0	4	77	11.7	1
67	12.6	14	77	12.5	12
67	13.3	19	80	12.1	8
69	11.6	9	82	12.0	6
72	12.9	13	87	13.8	15
65.1	12.4	..	77.2	12.6	..

That body weight influences the relative thickness of the long bones even within a species appears from the fact that the heavier males have higher average girth-trunk indices than the smaller females in every instance shown in table 10. This role of weight, however, is barely indicated in the series of 20 men listed in table 11, and should be tested on a larger series.

Age changes in the relative thickness of the long bones

Possible changes with age in the relative thickness of the long limb bones could be studied on only a limited material consisting of a few fetuses near term, some newborns and some very young infants, all belonging to the 4 genera of

higher primates listed in the tables 12 and 13. All these young specimens will here be simply referred to as "infants," even though they include some fetuses.

The girth-length indices of the infants are nearly always somewhat higher than the corresponding indices of adults in all 4 genera, as shown by the data in table 12. According to the averages in the last column this general age change is most pronounced in orang-utans and least in chimpanzees. For man such an age change has already been demonstrated by Nishizuka ('26), who found that at least in Japanese the long limb

TABLE 12

Age changes in the girth-length index. The values for adults are the means of males and females as given in table 1

GENUS	AGE	SPECIMENS	HU	RA	UL	FE	TI	FI	AVERAGE
Hylobates	inf.	7	15.3	11.3	10.0	16.4	16.7	10.2	13.7
	ad.	48	13.5	8.5	8.6	15.7	16.8	9.2	12.1
Pongo	inf.	8	24.7	19.3	19.2	31.6	27.8	17.4	23.3
	ad.	24	19.6	12.4	14.1	24.7	22.0	11.9	17.5
Pan	inf.	8	25.6	18.3	17.4	26.0	24.9	14.8	21.2
	ad.	26	25.3	17.2	17.4	25.6	25.2	14.2	20.8
Homo	inf.	5	22.5	19.9	19.6	22.6	26.1	13.6	20.7
	ad.	32	21.3	17.9	19.3	20.4	22.5	11.8	18.9

bones are slightly more slender in adults than in fetuses and infants. His, and also Bauer's ('40), data on the girth-length indices in human fetuses near term agree very closely with those obtained by the writer, in spite of the slight differences in the technique employed. It is of interest also to note that in the infants the ulna is not yet thicker than the radius, as it becomes in adults of all higher primates, but still shows the reversed relation, as in adults of all lower catarrhines.

The question, whether or not the circumferences of the long bones change in relation to trunk size during postnatal growth, can be answered by the data in table 13 which compare the girth-trunk indices of infants with those of adults. In the

anthropoids these indices decrease on an average with age, but in man they increase. To be more precise, only the orang-utan shows as marked a decrease in all indices as man shows an increase, whereas in gibbons and chimpanzees the age changes are neither uniform nor really significant. The author can offer no explanation for these findings which require further investigations.

TABLE 13

Age changes in the girth-trunk index. The values for adults are the means of males and females as given in table 8

GENUS	AGE	SPECIMENS	HU	RA	UL	FE	TI	FI	AVERAGE
Hylobates	inf.	7	12.6	9.2	8.1	11.7	10.0	6.1	9.6
	ad.	48	11.6	8.0	8.1	11.6	10.7	5.8	9.3
Pongo	inf.	8	18.1	13.5	13.4	17.1	13.6	8.5	14.0
	ad.	7	14.6	9.2	10.4	13.8	10.8	6.0	10.8
Pan	inf.	8	16.3	10.4	9.9	15.4	12.4	7.4	12.0
	ad.	20	15.8	9.7	10.0	15.5	12.8	7.2	11.8
Homo	inf.	5	10.2	7.0	6.9	12.3	11.7	6.1	9.0
	ad.	30	13.3	8.6	9.2	17.1	16.2	8.3	12.1

The relative thickness of the vertebrae

The relative thickness of the vertebral column is here represented only by the smallest transverse diameters of the bodies of the middle thoracic and middle lumbar vertebrae which are expressed in percentage of the trunk height. The averages of these indices in adult primates are listed in table 14. The relative thickness of the spine in the middle of the thoracic region amounts to only 2.4 in lemurs and to as much as 4.4 in tarsiers; the general average of this proportion for the recent prosimians equals 3.3. In the giant prosimian *Megaladapis* the writer was able to measure the minimal transverse diameters on one of the first few and on one of the last two thoracic vertebrae as 32 and 46 mm respectively, and it seems fully justifiable to assume that the corresponding measurement of the middle thoracic vertebra would be about half way between

TABLE 14

Averages of the vertebra-trunk indices in adult primates. The numbers of specimens are the same as in table 8

GENUS	SEX	THOR.	LUMB.
Tupaia	♀	4.0	4.8
	♂	3.8	5.0
Tana	♂	3.7	5.0
Lemur	♀	2.4	3.9
	♂	2.4	4.3
Microcebus	♀	3.0	3.9
	♂	3.0	3.9
Propithecus	♀	2.6	4.7
	♂	3.0	5.1
Daubentonia	♀	3.6	5.7
Nycticebus	♀	3.4	4.0
	♂	3.3	4.1
Perodicticus	♀	2.6	3.8
	♂	3.0	3.8
Galago	♂	2.7	4.2
Tarsius	♀	4.4	6.3
	♂	4.1	5.9
Seniocebus	♀	2.9	4.5
	♂	2.7	4.5
Oedipomidas	♀	2.8	4.1
	♂	2.9	4.5
Aotus	♀	2.7	4.3
	♂	2.2	3.7
Saimiri	♀	2.9	4.6
	♂	3.0	5.0
Cebus	♀	3.6	5.5
	♂	3.5	5.4
Alouatta	♂	3.4	5.0
Lagothrix	♀	3.9	5.1
	♂	3.8	4.7
Ateles	♀	3.8	4.9
	♂	3.6	5.2
Macaca	♀	3.3	5.2
	♂	3.3	5.4
Papio	♀	3.3	5.6
	♂	3.2	5.4
Cercocebus	♀	3.2	4.9
	♂	3.3	5.2
Cercopithecus	♀	3.5	5.3
	♂	3.3	4.7
Erythrocebus	♀	3.4	5.3
Pygathrix	♀	3.4	5.8
	♂	2.7	5.1
Nasalis	♀	3.1	5.0
	♂	3.1	5.7
Hylobates	♀	3.9	6.4
	♂	4.0	6.6
Symphalangus	♂	4.4	6.6
Pongo	♀	4.9	6.5
	♂	5.2	6.9
Pan	♀	4.4	6.4
	♂	4.5	6.7
Gorilla	♀	5.0	6.7
	♂	5.4	7.0
Homo	♀	5.2	7.8
	♂	5.5	8.2

these values or ca. 39 mm. As discussed earlier, the trunk height of *Megaladapis* must have measured somewhere near 630 mm, hence the thoracic vertebra-trunk index for this genus can be calculated as ca. 6.2, or certainly as very much more than in any of the small recent prosimians. In absolute size the vertebral bodies of *Megaladapis* surpass the corresponding bones in fully grown male gorillas, as shown by the example in figure 1 (D and G).

Among platyrrhines the thoracic vertebra-trunk index does not exceed 3.0 in the small forms (marmosets, *Aotus* and *Saimiri),* but lies above this figure in all the larger forms. In the lower catarrhines this index is surprisingly uniform, the averages varying only between 2.7 and 3.5.

Among the higher primates the small gibbons have thoracic vertebra-trunk indices which surpass those of all the monkeys, but are in turn surpassed by the corresponding values of the great apes and man. Man is distinguished in this respect by the highest of all values (among males), though male gorillas do not differ to a significant extent.

The lumbar vertebra-trunk index fluctuates among prosimians between less than 4.0 in *Perodicticus* and *Microcebus* and a maximum of about 6.0 in *Tarsius.* In platyrrhines this index does not rise above 5.0 in the smaller forms, but averages somewhat more in the larger ones. The catarrhine monkeys are again found to be quite uniform in relative vertebral thickness, the averages fluctuating between 4.7 and 5.8. In all the higher primates this index amounts to more than 6.0 and in man alone to more than 7.0. From table 14 it is seen that man is clearly distinguished among all primates by possessing the broadest lumbar vertebrae, relative to trunk height. Even the large male gorillas and orang-utans have relatively smaller lumbar vertebrae. That body weight cannot be the only factor in determining the relative thickness of the vertebral column is evident also from figure 2 which compares a human lumbar vertebra with that of a gorilla at least three times heavier, yet the corpus vertebrae of the latter is no larger than that of the small man. The writer inclines to the view that this human peculi-

arity of an exceptional relative thickness of the lumbar vertebrae represents an adaptation to the erect posture. The cumulative effect of the load carried by the upright spinal column requires the greatest strength or thickness at the base, as in a tree trunk. This view gains support from the observation that at least the lumbar spinal column is much thicker at its base

Fig. 2 Above middle thoracic and middle lumbar vertebrae of an adult male Negro weighing 55 kg and below corresponding vertebrae of an adult male gorilla whose skeleton is uniformly larger than that of another gorilla with known body weight of 165 kg.

compared to its cranial end in man [5] than in apes, as shown by the following few preliminary data: transverse diameter of first and of last lumbar vertebra in an adult man = 40 and 48 mm respectively, whereas in an adult gorilla = 42 and 45 mm, in a second adult gorilla 39 and 43 mm, in an adult chimpanzee = 30 and 33 mm and in an adult orang-utan = 32 and 35 mm (all male specimens).

TABLE 15

Age changes in the vertebra-trunk indices. The values for adults are the means of males and females as given in table 14. The numbers of specimens are the same as in table 13

GENUS	AGE	THOR.	LUMB.
Hylobates	inf.	6.0	9.2
	ad.	3.9	6.5
Pongo	inf.	6.9	10.2
	ad.	5.0	6.7
Pan	inf.	6.1	8.0
	ad.	4.4	6.5
Homo	inf.	6.3	9.4
	ad.	5.3	8.0

Sex differences in these vertebra-trunk indices occur in all the genera for which more than a few specimens and all of the same species could be studied in both sexes. The lumbar indices are larger in males than in the lighter females in all these groups and the thoracic indices in nearly all. The consistency of these sex differences in at least the higher primates is surprising inasmuch as the variability of these indices is very considerable. For instance, in man the thoracic vertebra-trunk index can vary between 4.7 and 6.2 in males and between 4.7

[5] Lanier ('39), by measuring the greatest transverse diameter of the caudal surface of vertebral bodies, found this width to increase from the first to the second last lumbar vertebra (the last is usually narrowed at its contact with the sacrum) from 49 to 55 mm in a large series of white males. The same measurements, taken by the writer on the corresponding vertebrae of a male gorilla, do not differ as much from each other, being 51 and 54 mm respectively.

and 5.7 in females and the lumbar index between 7.1 and 9.6 in the former and between 7.4 and 8.6 in the latter.

During postnatal growth the vertebra-trunk indices decrease very markedly in all the series which could be investigated, as shown by the data in table 15. In other words, the spinal column is proportionately very much thicker in infants than in adults in man as well as apes.

SUMMARY

In a total of over 350 primates the circumferences of the long limb bones at the middle of their shafts have been measured and expressed in percentage of the lengths of the bones (= girth-length indices). In 279 of these specimens the trunk height was determined so that the bone circumferences could also be calculated in their relation to the size of the trunk (= girth-trunk indices). The thickness of the spinal column was measured as smallest transverse diameter of the bodies of the middle thoracic and the middle lumbar vertebrae and these diameters were expressed in percentage of the trunk height (= vertebra-trunk indices). The relative lengths of the limbs and the body weight are also known in nearly all of this material and thus their influence on relative bone thickness could be analyzed by various comparisons.

The main results are briefly summarized as follows: the absolute thickness of the long bones of the limbs is closely dependent upon the load they have to support, but a gain in body weight is followed by a much smaller relative increase in bone girth, as is to be theoretically expected and has here been metrically demonstrated. A change in limb length does not primarily affect the absolute thickness of the limb bones, hence the girth-length indices become greater with a decrease in limb length and smaller with an increase in limb length, provided body weight remains practically unchanged. Infrequent and more or less marked exceptions to these general rules are probably connected with modifications in the main use of the limbs in supporting the body, such as leaping, brachiating and bipedal locomotion. Some of the larger systematic groups of

primates can differ somewhat regarding their general *relative* bone thickness, as measured by bone girth alone, possibly due to differences in the proportionate thickness of the compact walls, or in the density, strength and elasticity of the bony tissue.[6]

In all his girth-length indices man falls well within the range of variations of the corresponding indices among the other primates, but in his girth-trunk indices man is distinguished by the highest of all values for tibia and fibula combined with the second highest value for femur, undoubtedly on account of his bipedal locomotion. The leaping tarsier, too, has the highest girth-trunk indices for femur and tibia of all primates of similar small size and again because, as in man, the lower limbs alone carry the weight of the rest of the body. On the other hand, it may be due to some reduction in function that the girth-trunk indices are specially small for the leg bones of orang-utan and for the arm bones of man, considering the size of these primates.

The subfossil giant prosimian *Megaladapis* shows very clearly the effect of body size and of relative limb length on bone thickness. All limb bones of this unique primate have become very thick in response to the enormous load they have to carry, but those of the lower limbs appear to be particularly stout because these limbs have been very much reduced in proportionate length.

Of other findings relating to the relative thickness of the limb bones the following may here be summarized: in all higher primates the middle circumference of the ulna surpasses that of the radius, whereas in all Old World monkeys the reversed relation exists. All the higher primates possess remarkably thick fibulas (relative to trunk height), even the small gibbons surpassing other primates in this respect. Sex differences in the relative thickness of the limb bones favor males in all forms for which suitable material was available,

[6] Evans and Lebow ('52) have convincingly demonstrated that the physical properties of bone are far from uniform and can vary even regionally within one and the same limb bone.

the difference being particularly marked in types with great sex differences in body size. During postnatal growth the limb bones become more slender, but in relation to trunk height the bone girths decrease in orang-utans, they remain practically unchanged in gibbons and chimpanzees, and they increase in man.

The thickness of the vertebrae, measured as transverse diameters and expressed as percentage of the trunk height, is greater in all the higher primates than in any of the monkeys or in the recent prosimians with the exception of *Tarsius* which has unusually thick vertebrae. Within the major groups of primates the large types tend to show higher vertebra-trunk indices than the small ones, though there are some marked exceptions to this rule, notably *Tarsius* and man. Man is distinguished among all recent primates by having the proportionately thickest vertebrae, particularly in the lumbar region. Even the much heavier male gorillas do not equal man in relative thickness of lumbar vertebrae. This human specialization represents an adaptation to the upright posture and to the mechanical requirements of a true, perpendicular *column* of vertebrae. During postnatal growth the vertebra-trunk indices decrease very considerably in all the primates studied so far, i.e., the spinal column becomes proportionately more slender.

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HANDBOOK OF LATIN AMERICAN STUDIES: 1949. Francisco Aguilera, Editor. xii + 267 pp. University of Florida Press, Gainsville. 1952.— In this selective guide to material published in 1949 on Latin America, T. D. Stewart includes a summary of activity in the field of physical anthropology in Middle and South America during that year. Annotated bibliographic references to some 35 items completes the summary.

AAPA 1954 Annual Meeting.— The annual meeting of the American Association of Physical Anthropologists will be held at the Fels Research Institute, Yellow Springs, Ohio, on March 26 through March 28, 1954.

Scientific sessions will be held in the auditorium of the Fels Research Institute, and demonstrations will be given in adjacent conference rooms. The Fels Research Institute will be host to the association at a cocktail party to be given in the Fels Nursery School. The annual dinner will be held at the Antioch College Tea Room.

As a service to members planning to attend the meeting, arrangements will be made to meet trains at Xenia and Springfield, Ohio, and planes at the Dayton airport, Vandalia, Ohio. It is recommended that participants who plan to arrive by rail route their passage to Xenia (P.R.R.) or Springfield (N.Y.C.).

The Shawnee Hotel, Springfield, Ohio, will be the official hotel for the meeting. However, arrangements can be made for motel accomodations at the Knotty Pine, Anthony Wayne, or Tecumseh Motel upon request. It is advisable that requests for reservations be made by February 15.

In addition to the Fels Research Institute, members of the Association will have an opportunity to inspect the Antioch College anthropometric project and installations at Wright Field.

Inquiries relating to housing, transportation, or the program planning can be directed to Dr. Stanley M. Garn, Fels Research Institute, Yellow Springs, Ohio.

THE ORDER OF ERUPTION OF THE PERMANENT TEETH IN THE HOMINOIDEA

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TWO FIGURES

A clear-cut pattern of phylogenetic change is discernible in the sequence of eruption of the teeth of Primates, and particularly in that of the permanent teeth[1] (Schultz, '35, '49, '50a, b). In what is believed to be the most primitive arrangement, the first, second and third permanent molars appear in rapid succession before any deciduous teeth are lost. The deciduous incisors are then replaced by permanent ones; permanent premolars take the place of the deciduous molars; and the canines, the last teeth of the permanent set, then emerge. This sequence occurs in the tree shrews, whereas in the majority of prosimians, and in a few monkeys, the permanent incisors appear before the third molars, which precede the premolars and permanent canines. In most monkeys and in all the anthropoid apes, the third molar does not appear until the permanent premolars have erupted, while the second molar does not erupt until the permanent incisors are in place. In his 1935 paper, Schultz observes that in the apes the permanent canine very occasionally erupts after, and not before, the third molar, "but never as a sufficiently frequent occurrence to constitute a typical condition." A later chart which he has provided to illustrate the pattern of phylo-

[1] Schultz's description indicates that the pattern of phylogenetic change is not as conspicuous in the deciduous as in the permanent dentition. The order of eruption appears to be the same in catarrhine monkeys, in gibbons, and in modern man. In the three great apes, however, the milk canines invariably appear after the second milk molars, and not before, as in other Old World Primates.

genetic change shows the canine as the last tooth to erupt in the apes, Schultz ('50a) noting that its appearance relative to that of the third molar is variable. He also states that essentially the same sequence of dental eruption which characterizes most monkeys and the anthropoid apes occurs in fossil man and in a few groups of recent man.

The order of appearance of the permanent teeth in modern British children has lately been reassessed, and the opportunity taken to estimate the frequencies with which departures occur from the most usual pattern of eruption (Clements, Davies-Thomas and Pickett, '53a, b). The purpose of the present paper is to provide corresponding information for the chimpanzee and gorilla. To this end we have combined the detailed records tabulated by Schultz ('40) for 119 chimpanzees with incompletely erupted dentitions, and ('50b) for 86 gorillas, with our own observations made on 69 chimpanzee skulls (including three skulls without mandibles), and 80 gorilla skulls (including one skull without a mandible and one mandible without a skull), kept in the British Museum of Natural History and in the Birchington Collection.

METHODS

In both sets of records teeth were classified as non-erupted, when their crowns were below the level of the alveolar margin; as erupting, when the entire top of the crown was above the alveolar margin or, in the case of living and embalmed animals, had just pierced the gum; or as erupted, when the tooth was fully or almost completely in place.

The records of the dentitions seen on the right side of the skulls in the London and Birchington Museums were first subdivided into male and female groups. It was immediately apparent that there were no differences in the order of eruption which could be attributed to sex. The data were accordingly pooled. After both sets of records had been combined, they were sorted and classified in the order shown in tables 1, 2 and 3. The data for the upper and lower jaws were analyzed separately.

TABLE 1

The pattern of dental eruption in the chimpanzee

DENTAL PATTERN								NUMBER OF CASES							
								Upper jaw				Lower jaw			
I_1	I_2	C	Pm_1	Pm_2	M_1	M_2	M_3	Incompletely erupted		Fully erupted	Total	Incompletely erupted		Fully erupted	Tot
0	0	0	0	0	+	0	0	M_1		8	71	79	M_1	4	71	75
+	0	0	0	0	+	0	0	I_1		6	4	10	I_1	4	4	8
0	0	0	0	0	+	+	0			—	—	—		0	1	1
+	+	0	0	0	+	0	0	I_2 $I_1 + I_2$	2 3	5	8	13	I_2 $I_1 + I_2$	2 3	5	8	13
+	0	0	0	0	+	+	0			—	—	—	$I_1 + M_2$	2	0	2
0	0	0	+	+	+	0	0			0	1	1		—	—	—
0	0	0	0	+	+	+	0			—	—	—	$Pm_2 + M_2$	1	0	1
+	0	0	+	+	+	0	0			—	—	—		0	1	1
+	+	0	0	0	+	+	0	M_2 $I_1 + I_2 + M_2$	5 2	7	7	14	M_2 $I_1 + I_2 + M_2$	5 1	6	11	17
+	+	0	+	0	+	0	0			0	1	1		—	—	—
+	+	0	0	+	+	0	0			—	—	—		0	1	1
+	+	0	+	0	+	+	0	Pm_1 $Pm_1 + M_2$	2 1	3	1	4	Pm_1 $I_1 + I_2 + Pm_1 + M_2$	1 1	2	3	5
+	+	0	0	+	+	+	0			—	—	—	Pm_2	2	2	4
+	+	0	+	+	+	0	0			0	1	1		—	—	—
+	+	0	+	+	+	+	0	Pm_1 Pm_2 $Pm_1 + Pm_2$ M_2 $I_1 + I_2 + Pm_1 + Pm_2 + M_2$ $Pm_1 + Pm_2 + M_2$	4 1 2 1 1 1	10	17	27	Pm_1 $Pm_1 + Pm_2$ M_2 $Pm_1 + Pm_2 + M_2$	2 1 1 1	5	17	22
+	+	+	+	+	+	+	0	C		16	17	33	C	9	17	26
+	+	+	+	+	+	+	+	C M_3	1 1	2	1	3	C $C + M_3$	3 1	4	5	9

+ = Erupted tooth. 0 = Unerupted tooth.

RESULTS

Chimpanzees

Table 1, which summarizes the data for 188 chimpanzees whose permanent teeth were emerging, shows that in this species the first molar is invariably the first permanent tooth to erupt in both the upper and lower jaw. The central incisor is usually the next to appear. In one specimen (a mandible, Schultz, '40), this tooth was preceded by the second molar, which does not as a rule emerge until the lateral incisors have erupted. In another (also a mandible, C. 195 ♂, fig. 1), the central incisor was preceded by both the second molar and premolars (second on right side, first on left); and in a third (a maxilla, Schultz, '40), it was preceded by both premolars.

In the most usual sequence of eruption, the lateral incisors appear immediately after the centrals. In the three aberrant specimens already referred to, they were preceded (a) by the second molar; (b) by the second molar and first premolar on the left, and second premolar on the right side; and (c) by both premolars. In a further specimen (lower jaw, Schultz, '40) both premolars and the central incisors were out before the lateral incisors had started to erupt. In two other mandibles (M. 453 ♂ and M. 635 ♂, fig. 2), the second molars had appeared before the lateral incisors were through the alveolar margin.

The lateral incisors are usually followed by the second molars, and then the premolars. In three out of 17 maxillae, and two out of 22 mandibles, either one or other, or both premolars, preceded the second molars. In 6 out of 16 specimens the second premolar had begun erupting before the first. The occasional appearance of the premolars and second molars before the permanent incisors has already been noted.

The canine is almost invariably the penultimate tooth of the permanent set to emerge. The last tooth to break through

is the third molar, which, not infrequently, is fully erupted before the permanent canines are in their final position.

The order of eruption of the permanent teeth in the chimpanzee is therefore:

Usual order
upper and lower jaws: M_1 I_1 I_2 M_2 Pm_1 Pm_2 C M_3

Unusual orders
upper and lower jaws: M_1 I_1 I_2 Pm_1 Pm_2 M_2 C M_3

M_1 M_2 Pm_1 Pm_2 I_1 I_2 C M_3

The sign ⇌ indicates a possibility of variation in the order.

Gorilla

Table 2 summarizes the data for 168 gorillas whose permanent teeth were erupting, and shows that in this species, as in the chimpanzee, the first molar is invariably the first tooth of the permanent dentition to erupt. Unlike the chimpanzee, no instance was observed in which the second molar appeared before the central incisor, nor was there any specimen in which the eruption of the premolars had preceded that of the second molars. In 13 skulls the second premolars were in process of eruption before the first had broken through the alveolar margin, as compared with 4 in which the first were erupting before there was any sign of the second.

The permanent canine is as a rule the next tooth to appear, although in two instances the third lower molar had broken through the alveolar margin at an earlier stage.

The usual order of eruption of the permanent teeth in the gorilla is therefore:

Upper and lower jaws: M_1 I_1 I_2 M_2 Pm_2 Pm_1 C M_3

Table 3 summarizes the combined data for the eruption of teeth in chimpanzees and gorillas.

Order of appearance of upper and lower teeth. As Schultz points out, the lower teeth usually erupt before the upper, the difference being more regular and pronounced in the case of the molars than with the other teeth of the permanent

TABLE 2

The pattern of dental eruption in the gorilla

DENTAL PATTERN								NUMBER OF CASES							
								Upper jaw				Lower jaw			
I_1	I_2	C	Pm_1	Pm_2	M_1	M_2	M_3	Incompletely erupted		Fully erupted	Total	Incompletely erupted		Fully erupted	Total
0	0	0	0	0	+	0	0	M_1	5	33	38	M_1	11	32	43
+	0	0	0	0	+	0	0	I_1	4	3	7	I_1	3	6	9
+	+	0	0	0	+	0	0	I_2 $I_1 + I_2$ $I_1 + I_2 + M_1$	2 3 1 } 6	6	12	I_2 $I_1 + I_2$	2 4 } 6	5	11
+	+	0	0	0	+	+	0	M_2 $I_2 + M_2$	5 1 } 6	9	15	M_2 $I_2 + M_2$	4 1 } 5	12	17
+	+	0	+	0	+	+	0	Pm_1	1	1	2	$I_1 + I_2 + Pm_1 + M_2$	1	1	2
+	+	0	0	+	+	+	0	Pm_2	3	0	3	Pm_2	8	2	10
+	+	0	+	+	+	+	0	Pm_2 $Pm_1 + Pm_2$ $I_1 + I_2 + Pm_1 + Pm_2 + M_2$	4 7 1 } 12	16	28	Pm_1 Pm_2 $Pm_1 + Pm_2$	4 1 3 } 8	10	18
+	+	+	+	+	+	+	0	C	15	16	31	C $C + Pm_2$	8 1 } 9	7	16
+	+	0	+	+	+	+	+		—	—	—	M_3	2	0	2
+	+	+	+	+	+	+	+	C M_3 $C + M_3$	6 8 7 } 21	2	23	C M_3 $C + M_3$	7 15 14 } 36	2	38

+ = Erupted tooth. 0 = Unerupted tooth.

The pattern of dental eruption in the chimpanzee and gorilla

DENTAL PATTERN								NUMBER OF CASES							
								Upper jaw				Lower jaw			
I_1	I_2	C	Pm_1	Pm_2	M_1	M_2	M_3	Incompletely erupted		Fully erupted	Total	Incompletely erupted		Fully erupted	Total
0	0	0	0	0	+	0	0	M_1	13	104	117	M_1	15	103	118
+	0	0	0	0	+	0	0	I_1	10	7	17	I_1	7	10	17
0	0	0	0	0	+	+	0		—	—	—		0	1	1
+	+	0	0	0	+	0	0	I_2 $I_1 + I_2$ $I_1 + I_2 + M_1$	4 6 1 } 11	14	25	I_2 $I_1 + I_2$	4 7 } 11	13	24
+	0	0	0	0	+	+	0		—	—	—	$I_1 + M_2$	2	0	2
0	0	0	+	+	+	0	0		0	1	1		—	—	—
0	0	0	0	+	+	+	0		—	—	—	$Pm_1 + Pm_2$	1	0	1
+	0	0	+	+	+	0	0						0	1	1
+	+	0	0	0	+	+	0	M_2 $I_2 + M_2$ $I_1 + I_2 + M_2$	10 1 2 } 13	16	29	M_2 $I_2 + M_2$ $I_1 + I_2 + M_2$	9 1 1 } 11	23	34
+	+	0	+	0	+	0	0		0	1	1		—	—	—
+	+	0	0	+	+	0	0		—	—	—		0	1	1
+	+	0	+	0	+	+	0	Pm_1 $Pm_1 + M_2$	3 1 } 4	2	6	Pm_1 $I_1 + I_2 + Pm_1 + M_2$	1 2 } 3	4	7
+	+	0	0	+	+	+	0	Pm_2	3	0	3	Pm_2	10	4	14
+	+	0	+	+	+	0	0		0	1	1		—	—	—
+	+	0	+	+	+	+	0	Pm_1 Pm_2 $Pm_1 + Pm_2$ M_2 $Pm_1 + Pm_2 + M_2$ $I_1 + I_2 + Pm_1 + Pm_2 + M_2$	4 5 9 1 1 2 } 22	33	55	Pm_1 Pm_2 $Pm_1 + Pm_2$ M_2 $Pm_1 + Pm_2 + M_2$	6 1 4 1 1 } 13	27	40
+	+	+	+	+	+	+	0	C	31	33	64	C $C + Pm_2$	17 1 } 18	24	42
+	+	0	+	+	+	+	+		—	—	—	M_3	2	0	2
+	+	+	+	+	+	+	+	C M_3 $C + M_3$	7 9 7 } 23	3	26	C M_3 $C + M_3$	10 15 15 } 40	7	47

+ = Erupted tooth.

0 = Unerupted tooth.

dentition. This is borne out by table 4, which shows, for example, that in only one of 23 skulls in which the third molars were in process of eruption had the upper appeared before the corresponding lower tooth; that in 17 of 25 skulls, the lower incisors were in a more advanced stage of eruption than the upper; and that only in the case of the premolars were the upper teeth more advanced than the lower (25 of 37

TABLE 4

The presence and absence of corresponding teeth in the upper and lower jaws

TOOTH	JAW		CHIMPANZEE	GORILLA	CHIMPANZEE AND GORILLA	TOTAL
	Upper	Lower	No. of cases	No. of cases	No. of cases	
I_1	+	0	3	2	5	16
	0	+	7	4	11	
I_2	+	0	1	2	3	9
	0	+	4	2	6	
C	+	0	2	3	5	10
	0	+	2	3	5	
Pm_1	+	0	7	10	17	21
	0	+	3	1	4	
Pm_2	+	0	4	4	8	16
	0	+	5	3	8	
M_1	+	0	—	—	—	9
	0	+	2	7	9	
M_2	+	0	—	—	—	10
	0	+	9	1	10	
M_3	+	0	—	1	1	23
	0	+	6	16	22	

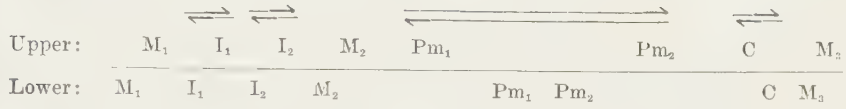
specimens). In 10 skulls the canines were erupting, and in 5 of these the upper teeth had appeared before the lower.

While the canines almost invariably appear before the third molar, they may not be fully in position by the time the third molars have erupted. Professor Schultz tells us that it is for this reason that he has indicated C and M_3 in parentheses in his later charts of dental eruption, to show their nearly

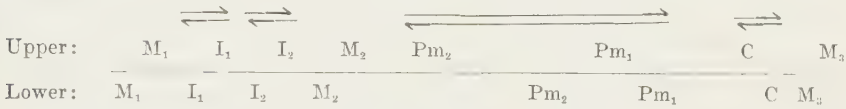
simultaneous eruption. He tells us, too, that the large canines of male apes are the last teeth of the permanent dentition to achieve their final position.

Taking both jaws together, the most usual observed sequence of eruption is:

Chimpanzee



Gorilla



DISCUSSION

The usual sequence of eruption is much the same in both African great apes and in both jaws (see table 3), but the order appears to be more constant in the gorilla than in the chimpanzee, in which the second molar, as already observed, may occasionally erupt before the incisors, or in which the premolars may sometimes begin erupting before the second molars. The second premolar more frequently precedes the first in the gorilla than in the chimpanzee.

These results confirm the general conclusions derived by Zuckerman ('28) from a study of 27 chimpanzee skulls with incompletely erupted permanent dentitions, and by Schultz ('35, '40, '50b), from his far more extensive studies. The only specimens in which Schultz found the second molars erupting after the premolars were animals which died in captivity, and in which the milk molars were shed at an early age. There were no specimens in our own series which showed the second molar erupting after the premolars. Schultz emphasizes the fact that in no gorilla which he examined had the premolars appeared before the second molars. This sequence was regarded as frequent by Krogman ('30), whose

observations otherwise fit in fairly well with the results of the present inquiry.

The usual order of eruption in the great apes differs greatly from that in modern British children (Clements, Davies-Thomas and Pickett, '53a, b). The most frequent sequence in children, as derived from the mean time of eruption, is:

Boys

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Mean age of eruption (months)	73	73	74	84	88	99	125	126	136	137	138	138	144	148	No obs.	
Upper:		M_1		I_1		I_2	Pm_1				C	Pm_2	M_2		M_3	M_3
Lower:	I_1		M_1		I_2			C	Pm_1	M_2				Pm_2		

Girls

Mean age of eruption (months)	69	70	71	80	84	94	113	118	126	128	133	134	138	140	No obs.	
Upper:			M_1	I_1		I_2		Pm_1		C	Pm_2		M_2		M_3	M_3
Lower:	I_1	M_1			I_2		C		Pm_1			M_2		Pm_2		

In 93 out of 2792 children examined the lower central incisor or the upper or lower first molar was the only permanent tooth that had erupted — a finding which indicates that the order of eruption of these teeth varies considerably in both boys and girls. The lower central incisor was the first tooth of the permanent dentition to appear in 50 of these 93 children; in 27 the first tooth was the lower first molar; and in 16 the upper first molar. No instance was observed in which it was the upper central incisor. In about one in 20 boys or girls the upper central incisor precedes the upper first molar, whereas in the lower jaw there is an equal chance of either tooth erupting first. This great variability in the start of the permanent dentition in modern man contrasts sharply with what is observed in the African great apes, in which the first tooth always seems to be the lower first molar.

In 45% of the children in whom only two permanent teeth had erupted, the teeth present were the upper and lower first molars. These are the first two teeth in 100% of apes. In children, again, the lower central incisor almost invariably appears before the upper; it does so in about only two of three chimpanzees or gorillas. Usually one or other premolar tooth erupts before the second molar in man, whereas the reverse order is the commonest in the anthropoids (all the exceptional orders occurred in captive apes). On the other hand, the variability in the usual order of eruption of the premolars and second molars, relative to one another, in the lower jaw, is probably no greater in man than in the apes, although it is much greater in the upper jaw. In man the time of appearance of the premolars appears to be influenced by the age at which the preceding milk molars are lost (Leslie, '51).

The order of appearance of the permanent canines constitutes the essential difference in the pattern of dental eruption in modern man and the African great apes. In modern man these teeth usually precede, whereas in the great apes they follow, the second molars and premolars. In British children today, a combination of erupted premolars and second molars, with the canines still unerupted, a pattern which is invariable in the great apes, is seen only in about 10% of cases in the upper jaw, and in 1% in the lower. In Old World monkeys, as contrasted with the great apes, the canines may very occasionally appear before the second premolars (Schultz, '33). In a radiological study of the rhesus macaque Baume and Becks ('50) have shown that the permanent second molars, the first and second premolars, and the permanent canines, erupt as a group. The first to appear is the mandibular permanent second molar, shortly followed by the corresponding maxillary tooth. A pause of variable duration then occurs before the deciduous molars and canines are replaced. The canines appear either before or after the second premolars, depending on the order, which is apparently completely variable, in which the milk canines and milk second molars are shed. Baume and Becks ('50) endorse Schultz's generalization

about the phylogenetic change which has occurred in the order of eruption of the permanent teeth in Primates, pointing out that modern man is characterized by a relative retardation in the eruption time of the accessional teeth (permanent molars), and a relative acceleration in that of the successional teeth (the teeth which replace their deciduous precursors).

It is usually stated that both Neanderthal Man and *Pithecanthropus pekinensis* differed from modern man, and agreed more with the modern great apes, in the precocious appearance of the second molars in relation to the canines (e.g. Weidenreich, '37; Bay, '46–'47; Schultz, '49). The order as given for fossil man by Weidenreich is:

$$M_1 \quad I_1 \quad I_2 \quad M_2 \quad Pm_1 \quad C \quad Pm_2 \quad M_3$$

This order is also said to be the usual sequence in Bushmen (Drennan, '32), and in Papuans and New Caledonians (Bay, '46–'47).

The small number of specimens on which conclusions about the sequence of dental eruption in primitive man are based makes it advisable to treat this generalization with reserve, as it is conceivable that random sampling might account for certain of the observations made. For example, the sequence observed by Drennan ('32) in each of the 4 lower jaws of Bushmen available to him, which showed the M_2 tooth as erupting before Pm_1 and Pm_2 or the canines, actually occurred in between 3 and 9% of cases of upper and lower jaws of the English children studied by Clements et al ('53a, b). Nevertheless, the data for primitive man, variable and few as they be, do conform more to the sequence characteristic of apes than of modern Englishmen.

Some interesting information is available about the order of eruption of the teeth in the Australopithecinae. Both jaws of *Australopithecus africanus* (the Taungs skull) had a complete set of deciduous teeth as well as the first permanent molars. This formula conforms to the unvarying pattern for the great apes, and to about 45% of modern British children. In the adolescent mandible of *Australopithecus prometheus*

described by Dart ('48), the second permanent molar, together with the first premolar on the left side, are fully erupted. The right first premolar is "only half-erupted and the second premolars have not as yet emerged from their eruption canals." This dental formula also conforms to the pattern usual in adolescent gorillas and chimpanzees; it would be expected to occur in no more than 1% of modern British children.

According to Broom and Robinson ('51, '52), the sequence of eruption of the permanent teeth in the fossils they have assigned to the species *Paranthropus crassidens* is (I_1, M_1), I_2, (C, P_1), M_2, P_2, M_3. They write that "The only variation that seems possible is between I_1 and M_1, C and P_1 and M_2 and P_2," respectively. Presumably this means that the possible sequence is M_1, I_1, I_2, P_1, C, P_2, M_2, M_3.

The only specific details about the dental formula of different specimens of *P. crassidens* which can be abstracted from Broom and Robinson's monograph are set out in table 5. The maxillary fragments have been labelled A p. 26, B p. 28, C p. 88, D p. 89, in the page-order in which they are referred to in the monograph. One maxilla referred to on p. 88 has been excluded from the table, as it is described only in these words: "we have a child upper jaw, which shows that the C (is) about to erupt about the same time as P_1, but probably a little earlier, and certainly long before P_2 or M_2." This specimen has been omitted, since experience has led us to be cautious about inferences regarding the probable time of appearance of teeth which have not yet erupted. Reliable conclusions about orders of eruption can be based only on the continuous study of the same individual, or on comparisons of the actual dental patterns in different specimens.

Three mandibles are referred to on page 88, of which only the first, designated E p. 88, is included in the table. The second and third, which have been omitted from the table, are described in the following terms: "we have a child jaw where M_1 and I_1 are both unerupted but where it seems probable that M_1 will erupt first. . . . We also have a mandible

TABLE 5

The dental formula in various specimens of Paranthropus crassidens, from Broom and Robinson ('52). The actual terms used to describe the presence or absence of the teeth are quoted as given

SPECIMENS	DECIDUOUS					PERMANENT							
	i_1	i_2	c	m_1	m_2	I_1	I_2	C	Pm_1	Pm_2	M_1	M_2	M_3
Maxilla													
A p. 26 "child of about 6 or 7 years." Both sides	Shed	Shed	Missing	"broken ... about to be shed."	"slightly worn."	"fully erupted, but has been damaged on both sides."	"fully erupted and the crown perfect."	"crown ... well developed, but still at a fairly high level in the bone."	"crown .. nearly ready to function."	Unerupted	"just come into use."	No information ...	
B p. 28 Child "corresponding to a modern female child of 11 years" Right side	.....	.....	... all shed	...	.....	.....	"preserved	sockets"	.....	"crown has probably cut the gum, but is not yet functioning."	Erupted	Erupted	No information.

Left side	.....	.....	.....	.....	...No information	.....	.....	.....	"there are preserved the second molar and part of the first molar."	.....	
C p. 88 "child maxilla" side not stated	No information		Shed	Shed	Shed	No information	"functioning"	"not yet functioning, but possibly having cut the gum."	No information	"scarcely worn."	No information
D p. 89 "a beautiful palate" Side not stated	.....	.....	shed	...	"still being used."	Erupted	Erupted	"both a little worn."	Unerupted	Erupted	"functioning . . practically unworn."	No information
						"We have a beautiful palate with all the permanent teeth functioning except P_2. (The third molar is not preserved in the specimen but almost certainly would be unerupted.)"					
Mandible E p. 89 "a child mandible" Side not stated	Shed	.....	No information		.....	"Erupting"	.....	No information	.....	"unerupted"	..no information

which shows that M_2 functions before P_2." The first of these two specimens has been omitted from table 5 for the same reason that we have excluded the maxilla already referred to. The second has been omitted as we are uncertain about the significance of the word "functions" in the context given.

The specimen we have designated A p. 26 is illustrated by Broom and Robinson in their text-figures 27, 28 and 29. They also "give a photograph of the upper side of the skull." The only one of the plate-figures which appears to correspond is plate 5, figure 18, which shows the basal surface of a skull of a child "probably . . . of about 7 yrs." It is impossible to make out from the photograph the teeth referred to in the text. The anterior half of the base is said to be "rather badly crushed but the left maxilla is almost complete. The right maxilla is badly crushed and not satisfactorily preserved."

The specimen referred to in our table as B p. 28 is illustrated in text-figure 30 and in a photograph, presumably plate 5, figure 19. There are certain discrepancies, however, between the textual description, the text-figure and the description and appearance of the photograph. The skull is said to be "much more severely crushed" than A p. 26, and in the text-figure it is referred to as an "adolescent female . . . of about 11 years of age." In the plate it is referred to as "about 13 years old." The text states that "On the left side there are preserved the second molar and part of the first molar." This description corresponds to the appearance of the photograph of the specimen, but text-figure 30 illustrates apparently intact and fully-erupted Pm_2, M_1 and M_2 teeth on both sides. The text refers to the first and second molars as being erupted on the right side; this corresponds to the appearance of the photograph. But according to the text, "the crown of the second permanent premolar has probably cut the gum, but is not yet functioning." This is not apparent on the photograph, which shows the better part of the occlusal surface of the tooth lying within the bone. In text-figure 30 the tooth is shown as fully erupted on both sides.

The description of mandible E p. 88 suggests that the central incisors were erupting before M_1 had appeared. Plate 1, figure 5, appears to be an illustration of this mandible, and according to the description "both the first permanent molars are still unerupted." The photograph shows, however, that the part of the jaw containing the molar teeth or their germs is missing on the right side, the side on which the central incisor has already appeared. According to the description of another *Paranthropus* specimen of the same dental age referred to in the text, but not included in our table, "it seems probable that M_1 will erupt first," that is, before the central incisor.

Four of the 5 specimens provide indications about the order of appearance of the premolars and second molars. The dental formula of A p. 26 is similar to that of any one of the African great apes at a corresponding stage of development. In B p. 28, the second permanent molars were fully in position before the second premolars; there is no sign of the first premolars or canines. We do not know how much weight to attach to the state of the alveolar margin, and the appearance of sockets, as indications that other permanent teeth had or had not erupted; and in any event the alveolar margin, judging from the photograph, was missing on the left side from in front of the first molar. C p. 88 presumably had its permanent canines, first premolar and first and second molars, with the second premolars "possibly having cut the gum." No information is provided about the third molars. In D p. 89, the second molar and canine appear to have erupted before the second premolar. To the best of our knowledge this sequence has never been observed in any gorilla or chimpanzee.

Unless there has been some confusion as between milk and permanent canines in the diagnosis of fragmentary teeth or sockets of teeth, it follows, therefore, that the order of eruption demonstrated by two of the fragments of *Paranthropus crassidens* about which information is given (D p. 89 and E p. 89) departs considerably from that characteristic of the African great apes, and conforms far more to the pattern

seen in modern Europeans. It is, however, difficult to see what evolutionary significance should be attached to the apparent sequence of eruption in these two Paranthropus specimens in view (a) of the fact that fossil Hominidae and certain existing groups of primitive man manifest practically the same order of dental eruption as do modern African great apes — particularly with respect to the appearance of the second molar relative to that of the canine, and (b) of the indication that in the fossils assigned to the related australopithecine genus, *Australopithecus prometheus,* the order of eruption was as in the modern great apes. It would be advisable to await further details about the dental pattern of the individual specimens of *Paranthropus* before reaching final conclusions.

SUMMARY

An analysis of the dental patterns of 188 chimpanzees and 166 gorillas whose permanent teeth were in process of eruption shows that the usual order of eruption in these animals is:

Upper:	M_1	I_1	I_2	M_2	Pm_1			Pm_2	C	M_3
Lower:	M_1	I_1	I_2	M_2		Pm_1	Pm_2		C	M_3

The sign ⇌ indicates a possibility of variation in the order.

A recent survey, of 2792 individuals, showed that the usual order of eruption in English children today is:

Boys

Upper:	M_1	I_1	I_2	Pm_1			C	Pm_2	M_2		
Lower:	I_1	M_1	I_2		C	Pm_1	M_2		Pm_2	M_3	M_3

Girls

Upper:		M_1	I_1	I_2	Pm_1		C	Pm_2	M_2		
Lower:	I_1	M_1		I_2	C		Pm_1	M_2	Pm_2	M_3	M_3

In man the permanent canines frequently precede the premolars, which in turn usually precede the second molars. It was found that the lower first molar had erupted first in 27 of 93 children with only one tooth erupted; the upper and lower first molar teeth were seen together in 45% of children with only two permanent teeth erupted. This variable picture contrasts with that seen in the great apes, in which the lower first molar always erupts first, and is invariably followed by the corresponding upper tooth. The lower incisor tooth erupts before the upper one in about two out of three apes, whereas the lower almost invariably appears first in man.

The sequence of dental eruption in modern man is very variable. It is therefore possible that variations attributable to random sampling may account for certain of the apparently aberrant dental patterns seen in the skulls of fossil man and in existing primitive peoples.

Observations relating to the sequence of dental eruption in the Australopithecinae are reviewed.

We are much indebted to Mrs. H. B. Powell-Cotton, Birchington, for allowing us to study her collection of anthropoid skulls, and to Mr. T. C. S. Morrison-Scott for giving us access to the collections of chimpanzee and gorilla skulls in the British Museum.

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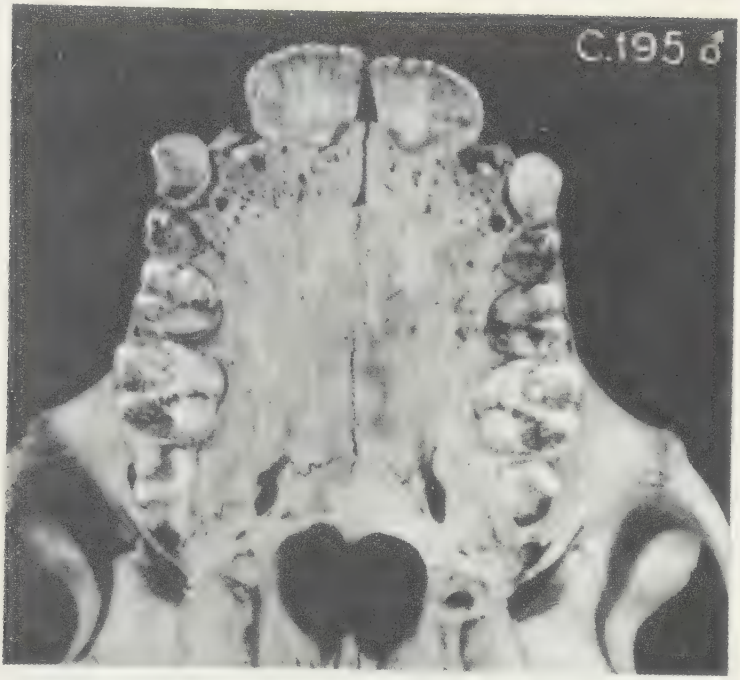
PLATES

PLATE 1

EXPLANATION OF FIGURE

1 Young male chimpanzee skull (Birchington C. 195) showing erupted lower right second premolar and lower left first premolar teeth with the second permanent molar teeth just erupting. The permanent incisors have not yet appeared.

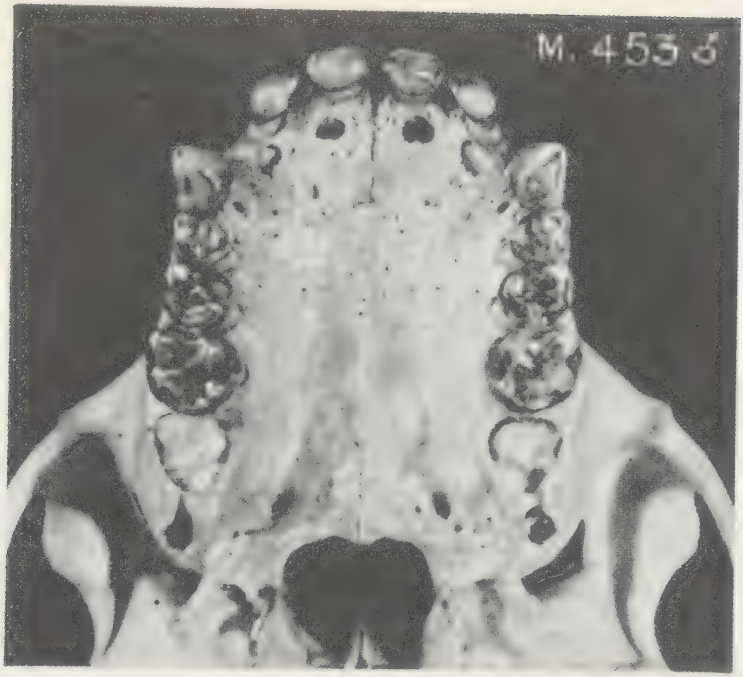

C.195 ♂

C.M.

PLATE 2

EXPLANATION OF FIGURE

2 Young male chimpanzee skull (Birchington M. 453) with the lower second molar teeth erupted before the permanent lateral incisors have emerged from the bone. Another mandible of a chimpanzee (Birchington M. 635) shows the same order of eruption.


M. 4533

CM

Maternal Nutrition and Child Health. By Kirsten Utheim Toverud, Genevieve Stearns and Icie G. Macy. National Research Council, Washington. vii + 174 pp. 1950. $2.00.— As a result of nutritional research and education, deficiency diseases in adults are rapidly diminishing in number, yet it is now apparent that a state of nutrition compatible with good health in the adult may be insufficient for the optimum development of the foetus, or the proper growth of the nursing child. The relationship between the nutritional status of the mother and the development of the infant before and after birth is, as the title suggests, the subject of this book. Prepared by outstanding specialists (including Norway's Kirsten Toverud), the specific nutritional requirements of pregnant and nursing mothers are discussed at length (78 pages). Evidence is cited to show that common neonatal disorders such as interocular, umbilical and intestinal hemorrhage may be due to maternal debility. Documentation is unusually complete (1008 references) and the citations obviously have been both read and digested. Finally, with a discussion of Scandanavian maternal health programs "Maternal Nutrition and Child Health" provides a broader coverage than previous American or British ventures along this line.— S. M. Garn.

PIGMENTATION IN A CENTRAL AUSTRALIAN TRIBE WITH SPECIAL REFERENCE TO FAIR-HEADEDNESS [1]

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THREE FIGURES

The occurrence of blondness in Australian aborigines has been recorded by a number of observers (Carmichael, 1878; Matthew, 1889; Stirling, 1896; Spencer and Gillen, 1899; Basedow, '25; Davenport, '25; Campbell and Lewis, '26; Hrdlička, '26; Taylor, '27; Spencer, '28; Campbell, Gray and Hackett, '36; Bates, '41; Birdsell, '50, and others). This condition is also illustrated without comment by Semon (1899), Spencer ('14), Basedow ('18), Dahl ('26), Spencer and Gillen ('27), Chewings ('36) and Mountford ('45). The fact is that those familiar with Central Australia in particular take fair-headedness so much for granted that it attracts no special attention (Mr. T. G. H. Strehlow, personal communication).

Birdsell ('50) gives the fullest account of this condition but uses his accumulated data in only a general way to illus-

[1] The material upon which this paper is based was collected on a University of Adelaide Anthropological Expedition financed largely be grants from the Wenner-Gren Foundation for Anthropological Research, New York, and by the University of Adelaide.

We are indebted to Mr. Langdon, Superintendent of the Yuendumu Settlement, and his wife, to Mr. and Mrs. Stafford, the school teachers, and to Mr. and Mrs. Fleming, the missionaries, who did everything possible to foster our inquiries. Dr. T. D. Campbell and Mr. Murray Barrett, members of the original expedition, returned to Yuendumu to extend their observations and were good enough to check some of ours. We are also indebted to Professor D. G. Catcheside, F.R.S., for his assistance with the genetics, and to Miss G. D. Walsh who took the photographs, matched the colors, and prepared the figures and tables for this paper.

trate his views on the "genetical concept of race," providing little in the way of usable detail. There does not appear to be any work devoted primarily to consideration of blondness as an event in itself within the framework of aboriginal pigmentation in general. The purpose of this paper is to provide such information — so far as the data permit — for a practically homogeneous group in Central Australia. Unfortunately, because adult males were the first to be examined, this possibility was not appreciated from the outset and some of the records are not as complete as they should be. However, they supply a more fully correlated account than has appeared hitherto and therefore have a value over and above that of merely indicating to future observers what to plan for in advance.

In 1926 Griffith Taylor described the blond aborigines he saw in Western Australia as "tawny," and Birdsell ('50) has coined the term "tawny gene" to express the hereditary mechanism producing the phenotype. It appears to the present writers, however, that "tawny" has only a limited application in describing this condition and, while "tawny gene" provides a convenient nomenclature and may finally prove scientifically justifiable, it contains a question-begging element which it seems best to avoid for the present.

MATERIAL AND METHODS

The tribal territory of the Ngalias lies in Central Australia, some 200 miles northeast of Alice Springs. Until only a few years ago this people lived in a completely tribal state: their admixture with neighboring tribes is no more than might occur under native conditions and their interbreeding with Whites is but slight. During the few years in which the tribe has congregated around the Government Settlement at Yuendumu, European attire of a sort has been adopted, the spoils of the chase are supplemented by Government rations and the young children have enjoyed the benefits of some schooling and improved diet. Nevertheless, much of the old life persists in the form of hunting trips, ceremonies and general way

TABLE 1

Skin and eye color — females

Skin color (inner arm)

AGE GROUP	REDDISH BROWN / RUSSET	DEEP RAW SIENNA / PROUT'S BROWN	RAW SIENNA / MUMMY BROWN	UMBER / BONE BROWN	BURNT UMBER / BLACKISH BROWN 3	VERY LIGHT VANDYKE / WARM SEPIA	LIGHT VANDYKE / MARS BROWN	VANDYKE / VANDYKE	TOTALS
< 1 yr.	....	....	....	....	....	1 (50.0%)	1 (50.0%)	....	2
1– 5 yrs.	....	....	1 (20.0%)	....	....	2 (40.0%)	2 (40.0%)	....	5
6–10 yrs.	....	1 (8.3%)	3 (24.9%)	....	....	7 (58.1%)	....	1 (8.3%)	12
11–15 yrs.	....	1 (14.3%)	3 (42.9%)	....	....	2 (28.6%)	1 (14.3%)	....	7
16–20 yrs.	....	....	2 (25.0%)	....	....	3 (37.5%)	....	3 (37.5%)	8
21–30 yrs.	....	....	....	....	....	6 (85.8%)	....	1 (14.3%)	7
31–40 yrs.	....	....	....	1 (14.3%)	....	5 (71.5%)	1 (14.3%)	....	7
41–50 yrs.	....	....	1 (100.0%)	....	....	....	....	....	1
> 50 yrs.	....	....	1 (33.3%)	....	....	2 (66.6%)	....	....	3
		2 (3.9%)	11 (21.2%)	1 (1.9%)		28 (53.8%)	5 (9.6%)	5 (9.6%)	
Totals			14 (26.9%)				38 (73.1%)		52

Eye color

< 1 yr.	....	....	....	....	1 (50.0%)	1 (50.0%)	....	....	2
1– 5 yrs.	....	....	....	1 (25.0%)	2 (50.0%)	....	....	1 (25.0%)	4
6–10 yrs.	....	....	2 (16.6%)	5 (41.5%)	2 (16.6%)	....	....	3 (24.9%)	12
11–15 yrs.	....	....	2 (28.6%)	....	4 (51.2%)	....	....	1 (14.3%)	7
16–20 yrs.	....	....	1 (12.5%)	1 (12.5%)	5 (62.5%)	1 (12.5%)	....	....	8
21–30 yrs.	....	....	2 (33.4%)	1 (16.7%)	2 (33.4%)	1 (16.7%)	....	....	6
31–40 yrs.	....	....	4 (57.2%)	1 (14.3%)	1 (14.3%)	....	....	1 (14.3%)	7
41–50 yrs.	....	....	1 (100.0%)	....	....	....	....	....	1
> 50 yrs.	....	....	1 (50.0%)	....	....	....	....	1 (50.0%)	2
	....	....	13 (26.5%)	9 (18.4%)	17 (34.7%)	3 (6.1%)	....	7 (14.3%)	
Totals			39 (79.6%)				10 (20.4%)		49

of life; and these people may still be accepted as a reasonable example of aborigines not yet materially affected by their relatively minor change in environment.

The tribe comprised some 300–400 members of all ages. Of these over 100 were examined and the sample may be considered quantitatively adequate. Every effort was made to include proper representation of both sexes at all ages but the majority of adolescent males were away hunting or at work, so that the number examined in this group was too small to provide a strictly random sample. This is the more regrettable since adolescent males might have provided some valuable information. However, the gap can be broadly covered by judicious intrapolation. All White crosses were avoided but it was not possible to avoid a few extra-tribal inhabitants and inter-tribal crosses since the genealogical tables compiled were not generally available until after the examination was completed. Such exotic elements are shown in figure 1, but for the most part they are included in the consolidated data since they are from closely allied peoples and could not be shown to betray any significant differences.

For the purpose of examination each aborigine was stripped completely naked. In the present context records were made of skin and iris color, and of the color of the hair on different parts of the body.

Skin color was judged by matching against a set of standards devised by Campbell and Hackett ('27). Observations were made on both the forehead and the inner side of the upper arm. Since the people now habitually go clothed the more exposed forehead might be expected to be the darker but this was so in only a few cases. For the sake of uniformity, however, the inner arm was always taken as the standard for skin pigmentation. In view of the notorious difficulty of classifying any colors (see, e.g. Trotter, '39; Gates, '52, and others) it was felt best to adhere to the standards of Campbell and Hackett but, since standards change with time and exposure, these were reassessed by the artist on the basis of pigment content and named, so far as possible, according

to current usage. The colors were also matched against the Ridgway ('12) standards. These have been carefully preserved and appear to be in good condition but the possibility of deterioration during the past 40 years cannot be excluded. Consequently, all that is claimed here is that the colors given are those determined by matching against a particular standard at a particular time and place. In tables 1, 2, and 3 the upper color is the artist's match, the lower is the Ridgway equivalent.

Iris color was determined by matching against a set of artificial eyes previously employed by Campbell, Gray and Hackett ('36). These, too, were reconstructed by the artist and given both their common name and the Ridgway equivalent. The results are subject to the same qualifications as with skin colors. Unfortunately, a number of individuals suffered bilateral corneal opacities of traumatic origin, which precluded any possibility of observation.

Hair color was assessed by simple observation as white, grey, ash-blond to light brown, light brown, medium brown, dark brown and black. In many instances — as previous observers have noticed — the color was not uniform along the length of the hair. In particular, in the lighter grades the root was usually darker than the remainder. In these cases the classification adopted was that of the predominating color. Sometimes adequate simple assessment was impossible and this difficulty was overcome in the subsequent broad analysis into "fair" and "dark."

Whenever classification of color raised any substantial difficulty the final decision was made by agreement between two or more independent observers.

RESULTS

Skin color

The findings in males and females according to age groups are shown in tables 1 and 2, and the combined data in table 3.

TABLE 2

Skin and eye color — males

Skin color (inner arm)

AGE GROUP	REDDISH BROWN / RUSSET	DEEP RAW SIENNA / PROUT'S BROWN	RAW SIENNA / MUMMY BROWN	UMBER / BONE BROWN	BURNT UMBER / BLACKISH BROWN 3	VERY LIGHT VANDYKE / WARM SEPIA	LIGHT / MARS BROWN	VANDYKE / VANDYKE	TOTALS
< 1 yr.	....	....	....	....	....	....	....	....	0
1– 5 yrs.	....	....	....	....	....	4 (80.0%)	....	1 (20.0%)	5
6–10 yrs.	....	1 (11.1%)	2 (22.2%)	1 (11.1%)	....	5 (55.5%)	....	....	9
11–15 yrs.	....	....	2 (50.0%)	....	....	1 (25.0%)	....	1 (25.0%)	4
16–20 yrs	....	....	....	....	....	....	1 (100.0%)	....	1
21–30 yrs.	....	....	....	1 (16.7%)	....	3 (50.1%)	....	2 (33.4%)	6
31–40 yrs.	....	....	2 (40.0%)	....	....	2 (40.0%)	....	1 (20.0%)	5
41–50 yrs.	....	....	1 (50.0%)	....	....	....	1 (50.0%)	....	2
> 50 yrs.	....	....	....	3 (30.0%)	....	4 (40.0%)	2 (20.0%)	1 (10.0%)	10
		1 (2.4%)	7 (16.8%)	5 (12.0%)		19 (45.6%)	4 (9.6%)	6 (14.4%)	
Totals			13 (31.0%)				29 (69.0%)		42

Eye color

AGE GROUP	REDDISH BROWN / RUSSET	DEEP RAW SIENNA / PROUT'S BROWN	RAW SIENNA / MUMMY BROWN	UMBER / BONE BROWN	BURNT UMBER / BLACKISH BROWN 3	VERY LIGHT VANDYKE / WARM SEPIA	LIGHT / MARS BROWN	VANDYKE / VANDYKE	TOTALS
< 1 yr.	....	....	....	....	....	....	....	....	0
1– 5 yrs.	1 (20.0%)	....	....	2 (40.0%)	1 (20.0%)	1 (20.0%)	....	....	5
6–10 yrs.	....	....	3 (33.3%)	....	4 (44.4%)	....	....	2 (22.2%)	9
11–15 yrs.	....	....	1 (25.0%)	....	....	....	....	3 (75.0%)	4
16–20 yrs.	....	....	....	....	1 (100.0%)	....	....	....	1
21–30 yrs.	....	....	1 (16.7%)	....	4 (66.8%)	....	1 (16.7%)	....	6
31–40 yrs.	....	....	3 (60.0%)	....	2 (40.0%)	....	....	....	5
41–50 yrs.	....	1 (50.0%)	1 (50.0%)	....	....	....	....	....	2
> 50 yrs.	....	2 (25.0%)	2 (25.0%)	3 (37.5%)	1 (12.5%)	....	....	....	8
	1 (2.5%)	3 (7.5%)	11 (27.5%)	5 (12.5%)	13 (32.5%)	1 (2.5%)	1 (2.5%)	5 (12.5%)	
Totals			33 (82.5%)				7 (17.5%)		40

TABLE 3

Skin and eye color

Consolidated data — males and females

AGE GROUPS AND SEX	Yellow Red Black		Skin color (inner arm)				Red Black		TOTALS	
	REDDISH BROWN	DEEP RAW SIENNA	RAW SIENNA	UMBER	BURNT UMBER	VERY LIGHT VANDYKE	LIGHT VANDYKE	VANDYKE		
	RUSSET	PROUT'S BROWN	MUMMY BROWN	BONE BROWN	BLACKISH BROWN 3	WARM SEPIA	MARS BROWN	VANDYKE		
Female children	....	2 (5.9%)	9 (26.5%)	....	....	15 (44.1%)	4 (11.8%)	4 (11.8%)	34	
Female adults	....	....	2 (11.1%)	1 (5.6%)	....	13 (72.2%)	1 (5.6%)	1 (5.6%)	18	52
Male children	....	1 (5.3%)	4 (21.2%)	1 (5.3%)	....	10 (52.6%)	1 (5.3%)	2 (10.6%)	19	
Male adults	....	....	3 (12.9%)	4 (17.2%)	....	9 (38.7%)	3 (12.9%)	4 (17.2%)	23	42
	....	3 (3.2%)	18 (19.1%)	6 (6.4%)	....	47 (49.8%)	9 (9.6%)	11 (11.7%)		
Totals			27 (28.7%)				67 (71.3%)			94
					Eye color					
Female children	....	....	5 (12.2%)	7 (21.2%)	14 (42.4%)	2 (6.1%)	....	5 (15.2%)	33	
Female adults	....	....	8 (50.0%)	2 (12.5%)	3 (18.8%)	1 (6.3%)	....	2 (12.5%)	16	49
Male children	1 (5.3%)	....	4 (21.2%)	2 (10.6%)	6 (31.8%)	1 (5.3%)	....	5 (26.5%)	19	
Male adults	....	3 (14.3%)	7 (33.3%)	3 (14.3%)	7 (33.3%)	....	1 (4.5%)	....	21	40
	1 (1.1%)	3 (3.4%)	24 (26.6%)	14 (15.7%)	30 (33.7%)	4 (4.5%)	1 (1.1%)	12 (13.5%)		
Totals			72 (80.9%)				17 (19.1%)			89

It will be noted that the colors fall into two major groups. One is composed of red, black and yellow — mainly siennas and ambers; the other of red and black only — a series of vandykes. In both sexes at practically all ages the vandykes predominate markedly. In females the ratio is nearly 3:1, in males about 2:1. Here a larger sample might either eliminate or intensify any sexual distinction. This color grouping is not, however, absolute. Although in the majority of cases

TABLE 4

Head hair color according to age and sex

AGE GROUP	SEX	"FAIR"	"DARK"	TOTALS
0–10	F	17 (85.0%)	3 (15.0%)	20
	M	16 (84.2%)	3 (15.8%)	19
11–20	F	14 (93.3%)	1 (6.7%)	15
	M	0 (0.0%)	9 (100.0%)	9
21–30	F	4 (66.7%)	2 (33.3%)	6
	M	0 (0.0%)	6 (100.0%)	6
31–40	F	1 (16.7%)	5 (83.3%)	6
	M	0 (0.0%)	5 (100.0%)	5
41–50	F	2 (66.7%)	1 (33.3%)	3
	M	0 (0.0%)	2 (100.0%)	2
51–60 +	F	1 (33.3%)	2 (66.7%)	3
	M	2 [1] (25.0%)	6 (75.0%)	8
Totals	F	39 (68.4%)	14 (31.1%)	53
	M	18 (31.6%)	31 (68.9%)	49
Totals		57 (55.9%)	45 (44.1%)	102

[1] See text: these may be artefacts.

the forehead and arm colors fell into the same series, some differed and then one might fall into the alternative series.

There is some — not very definite — indication of a darkening in general coloration with age but it cannot be asserted with any confidence that the males are darker than the females at any age.

The palms and soles, when clear, were distinctly paler than the skin surface generally. No trace of albinism was en-

countered, nor was there any evidence of a "mongolian spot" (tâche pigmentaire) in the young children who were examined.

Since these aborigines have adopted some European attire, they have become subject to sunburn on prolonged unaccustomed exposure to sunlight.

Eye color

This is classified under the same general headings as the skin color (tables 1, 2, and 3). The distribution was not so clear-cut, however. Some of the colors were matched best when a trace of blue was added to provide the basic blue of the iris. When this blue was eliminated the residual color — representing the secondary pigmentation to be assessed — was more readily encompassed by the classification adopted here.

With this qualification the colors fell into the same two groups as the skin but the bias was changed, the + yellow series predominating. In both sexes, and in the consolidated data, the ratio was approximately 4 : 1. Raw sienna (mummy brown) and burnt umber (blackish-brown 3) were the most common colors.

It was not possible to establish any correlation of iris color with skin color, or with age or sex. No blue irides were observed in either sex at any age, nor was there any evidence of senile recession or fading of secondary pigment to expose the blue of the iris.

Hair color

Before puberty this was observable only in the head hair, brows, lashes and fine body hair; in adolescents and adults beard, and pubic and axillary hair were added.

Some points may be disposed of immediately. In all cases, irrespective of age or sex, the eyebrows and lashes were dark brown to black. In both sexes the pubic hair from its first appearance was always dark brown to black (fig. 1). In all males and in the majority of females the axillary hair from

its first appearance was dark brown to black, but in a few females it was rather lighter — medium brown.

In the case of head hair: from ash-blond to light brown is broadly classed as "fair," from medium brown to black as "dark." The incidence of hair color according to age and sex is given in figure 1. This shows a general shift from

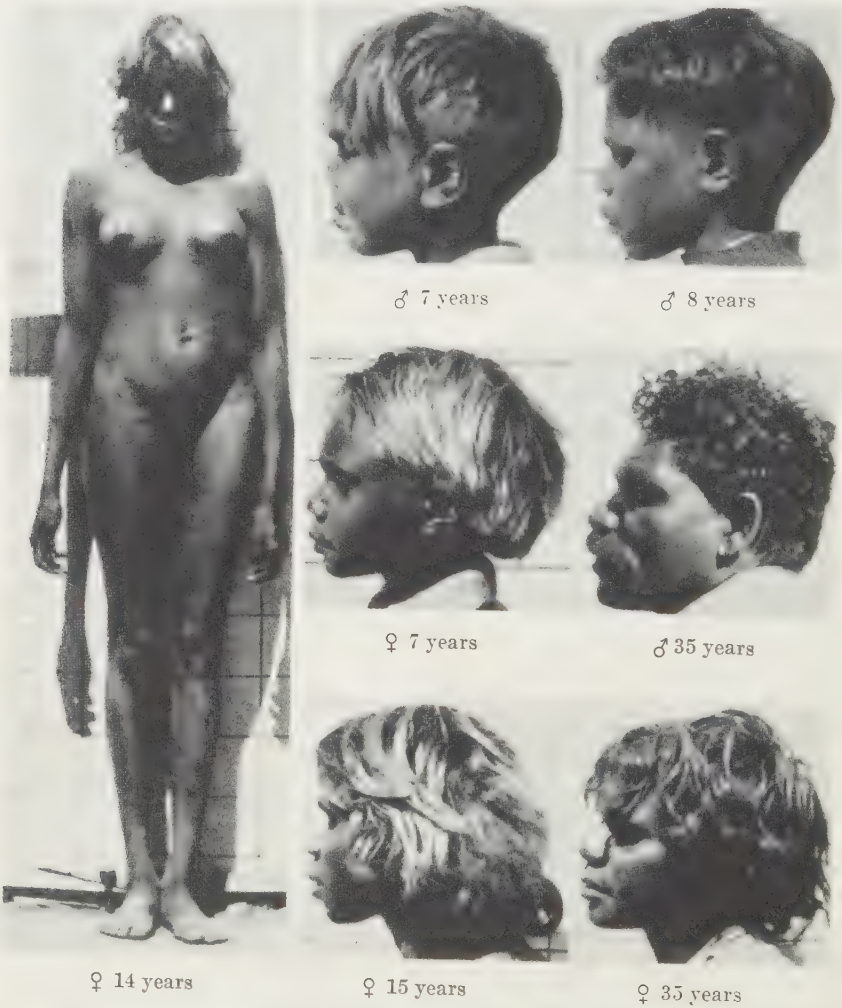
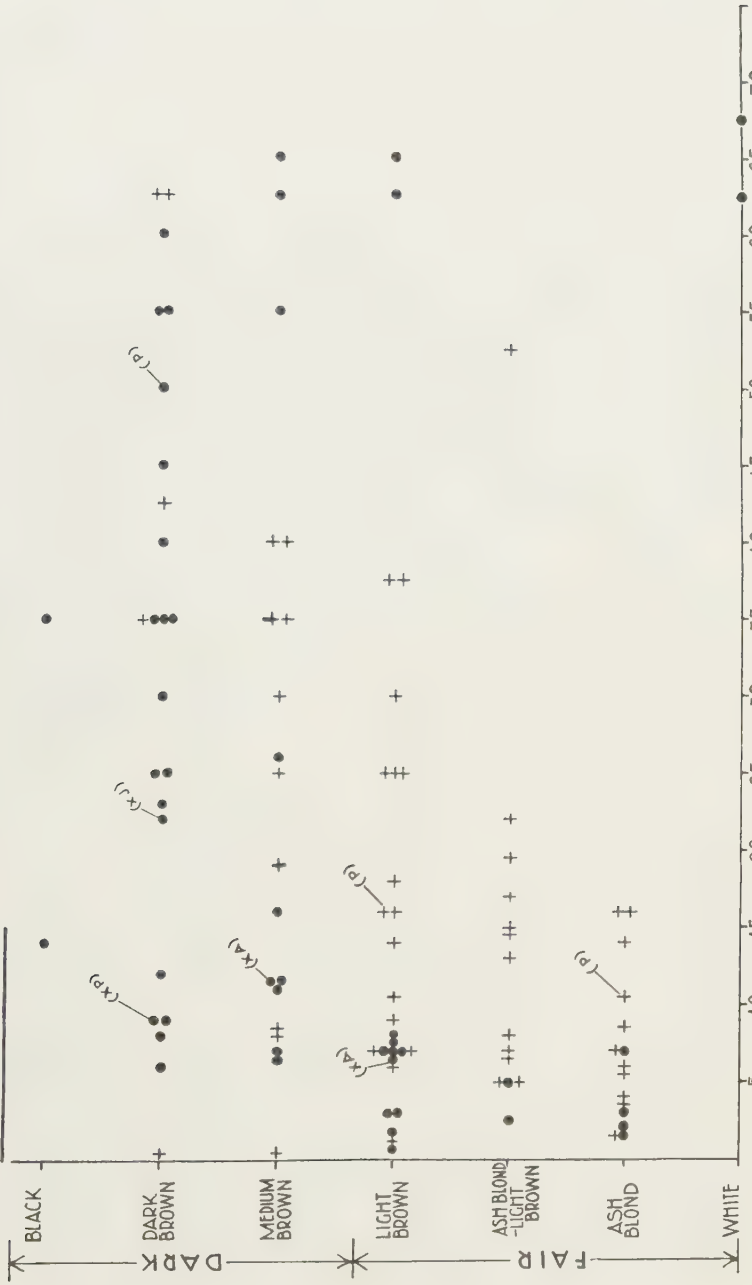


Fig. 1 Examples of fair-headed and dark-headed aborigines from Yuendumu.



All Ngalia except:- (P)=Pure Pintubi, (xP)=Ngalia × Pintubi cross, (x A)=Ngalia × Aranda cross, (x J)=Ngalia × Jumu cross

Fig. 2 Age distribution of head hair color in 102 Yuendumu aborigines.

"fair" to "dark" in both sexes with increasing age, but the shift is much more abrupt in the males than in the females. Dissection into age groups according to sex (table 4) illustrates this point more precisely. Up to 10 years of age the color distribution is approximately the same in both sexes at about 85% "fair" to 15% "dark." Over the age of 11 years it is difficult to find a "fair" male while female "fairness" falls off more gradually. Taken over all the females provide about two-thirds of the "fair" total, the males approximately the same proportion of the "dark" total. The figures on the individual age groups are, unfortunately, too small to give more than a general picture of the total trend.

In the males the onset of darkening becomes apparent from about the 8th year. In adolescence the hair ranges from medium brown to black (observations in this group are very limited) while beyond 20 years practically all are in the "dark" category. In the case of the two old men classified within the "fair" group it is possible that constant application of grease and ochre has obscured the natural trend. In the females darkening becomes definite only after about the 20th year, and even in old age does not often exceed light brown. Not infrequently the same hair ranged from very fair at the tip, through light brown to a medium brown root. Contrary to the findings of most previous observers a red element was occasionally observed in the blond hair which then had a golden tinge.

Attention may be drawn to the single female infant of three weeks whose head hair was dark brown (fig. 1). Whether this was a persistent lanugo is uncertain — the body hair was too sparse to record. The mother of this child had light brown head hair and fair body hair. The father was not observed.

In both males and females the general body hair remained fair until after puberty, except in the single case of a boy of 8 years whose head hair was already dark brown. Beyond that age observations on general body hair are limited but, so far as they go, they indicate a progressive darkening of body hair with head hair in males — every adult male so

recorded had dark body hair. In all the adult females observed, however, the body hair was fair, even beyond the age of 50 years. As with head hair, there was occasionally a golden tinge in the body hair, indicating some red pigment.

The beard was observed whenever possible but many of the adult males were shaven (or plucked) fairly clean. Generally, some beard formation could be detected in males from the age of two years. Correlation with hair color — where the comparison was made — varied, but more so under the age of 20 years than later. Under 20 years the beard was lighter than the head in 4 instances, the same in 8, and darker in 5; over 20 years no beard was lighter than the head, 13 were the same, and two darker. Beard color ranged from light brown to black. The lighter colors were common in young males and it seems likely that the beard shows to some extent the general tendency to darken with age. Of 54 females only three showed definite beard formation — all medium brown in color. The youngest, aged two years, had ash-blond head hair; the other two, aged 35 and 40 respectively, had head hair of the same medium brown.

Greying of the hair was not observed in any of the females although some exceeded 60 years of age. In the males the beard starts to turn grey from about 40 years, but one young man of 22, with dark brown head hair, had a white (shaven) beard. Greying of the head starts at about 55 years. The beard is completely white at 65 years, the head later.

No correlation was established between the incidence of blondness on the one hand and pigmentation of skin or iris on the other. Nor was there any clear-cut correlation between blondness and texture or form of hair. Hair texture ranged from fine to medium for the most part in both sexes at all ages; coarse hair was noted in only three instances — in one young female, and in one young and one adult male. In childhood in both sexes hair form was usually from straight to a light wave, but in adults there is a shift towards deeper waves or even curls, more marked in males than in females.

Hair quantity ranged from sparse to medium, according to situation. On the scalp the quantity was moderate to medium, irrespective of age, sex, or pigmentation. The fine body hair was sparse to medium in females and slightly more abundant in males. Brows, lashes, beard, axillary and pubic

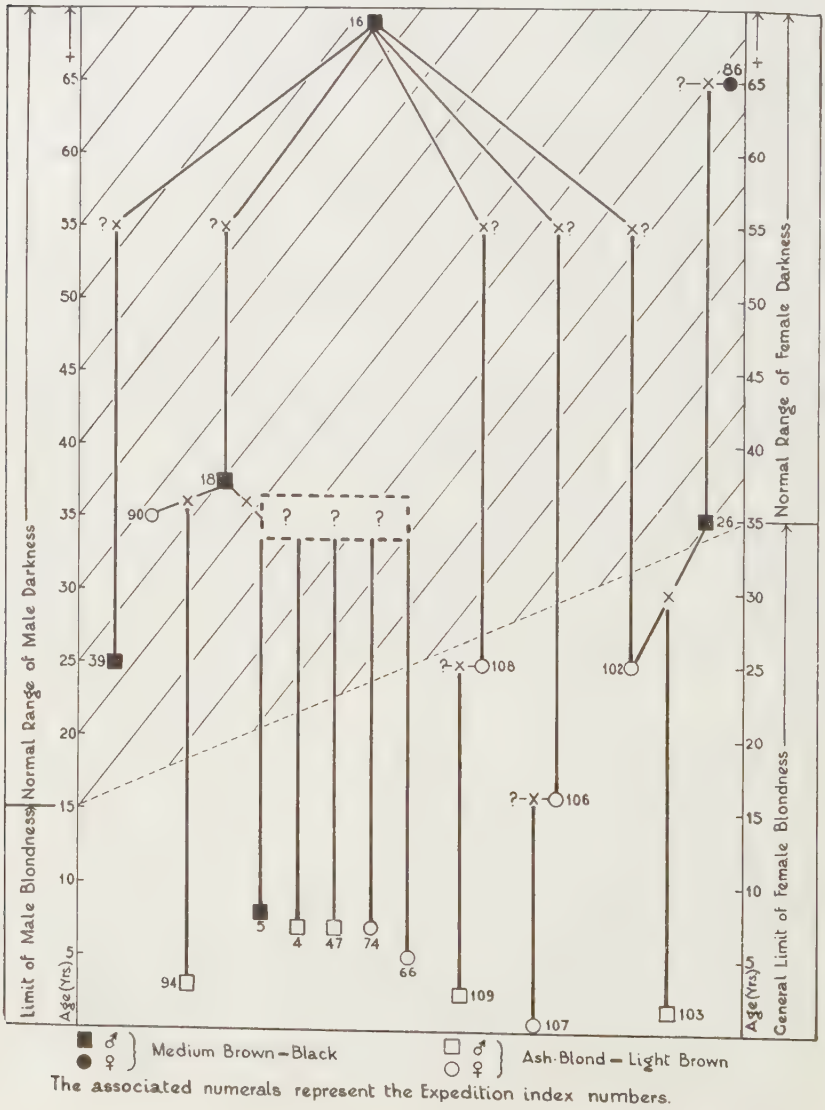


Fig. 3 Incomplete genealogical table of inheritance of head hair color.

hair were all only moderate in amount. Some baldness was noted in one male at 55 years but was not general under 60 years; one female over 60 years showed a small amount of baldness.

DISCUSSION

Skin pigmentation as found here conforms to the general Central Australian standard described by Spencer and Gillen (1899), Campbell, Gray and Hackett ('36) and others, but the intensification with age described by the latter authors could not be positively established. Semon (1899) mentions geographical variations in skin coloration. Other observers have stated that intensity varies with latitude, being greater in the north than in the center or south. This has been considered (e.g. by Howells, '37; Birdsell, '50) evidence of a different ethnological origin but it could equally well be regarded as the expression of a cline of pigmentary variation with temperature and humidity, such as Huxley ('42) has described for other warm-blooded animals. Other possibilities are obvious. No tâche pigmentaire was detected in the very young. Basedow ('25) does not mention this as a feature of very young aborigines nor do Cleland and Hackett ('27) in their account of a newly-born full aborigine. The tâche does not appear to be a characteristic of the Australian aborigine.

The iris color of these aborigines falls within the range previously described by Wood Jones and Campbell ('24), Basedow ('25), Davenport ('25), Campbell and Lewis ('26), Campbell, Gray and Hackett ('36), and others. There was no case of blue iris such as Basedow ('25) found in a young female, nor any senile fading to blue as described by Davenport ('25).

In the case of the hair: the eyebrows, lashes, axillary and pubic hair, as well as the hair of the beard and scalp in adult males, gave no cause for comment. These all conformed to the accepted aboriginal pattern — there was not even a single case of light-haired eyebrows like those found by Campbell and Lewis ('26) in a small group at Ooldea. Up to this point, then, these aborigines are sufficiently conventional to exclude

fairly confidently any degree of albinism — even partial as described by Harris ('26) for the San Blas Indians. Basedow ('25), indeed, has pointed out that no authentic case of albinism has ever been described in Australian aborigines. Equally, blondness cannot be due to any European admixture as postulated by Mrs. Daisy Bates ('41) and suspected by others. Davenport ('26) has shown that such intermixture in aborigines produces other pigmentary changes, e.g. in the iris and skin. It seems evident that hybridism of a sufficient potency to produce such a change in head hair could scarcely miss the brows, lashes, beard, etc., especially when it is recalled that fairness is usually recessive to darkness.

It might be argued that, since hair color and hair wave both intensify with age, there is some correlation between pigmentation and hair form. However, Campbell, Gray and Hackett ('36) found a similar intensification of wave with age in groups devoid of blondness, so the possibility of such association seems negligible.

According to Basedow ('25) the aborigine is born covered with a fair "lanugo" which later becomes stronger and black. However, the newly-born infant described by Cleland and Hackett ('27) had black hair, and the only really young member of this series — a female aged three weeks — was also dark. It is possible that the infants, like the adults, of different parts of Australia differ in this respect. Alternatively, as in many blond Europeans, the true lanugo hair may be dark and the permanent hair fair. At all events, the bulk of the children are decidedly fair-haired at a slightly greater age (table 4; fig. 2). All in this tribal group showed some darkening with the passage of time although in other groups, apparently, blondness may persist through maturity until the hair turns grey (Mr. N. B. Tindale, personal communication).

It seems clear that, in the aborigines under discussion, blondness is purely incidental, being a strictly localized, or particulate, intrusion upon the total aboriginal pattern. An interesting point is that the blondness is gradually lost with age. This is a not uncommon event in Europeans since, as

Stern ('49) points out, the phenotype for hair color is not necessarily static.

There appear to be two factors determining the aboriginal hair coloration — one genetic, the other contained in the bodily environment and possibly hormonal in nature. So far as the genetic factor is concerned the best working hypothesis appears to be that which invokes a single gene mutation, as Birdsell ('50) has proposed. His isophenic map for this "tawny" gene shows a varying intensity of expression radiating from a maximum in the southwest of Central Australia. (It may be mentioned that Birdsell's isophenic map requires revision since Mr. C. P. Mountford informs us that blondness is also common in Arnhem Land.) It is possible, but unlikely, that the somatic environmental factor varies. More probable is the hypothesis of genetic spread from the region of maximum incidence, as Birdsell suggests. He considers the "tawny" gene a partial dominant; one of the present writers, then in ignorance of Birdsell's work, has suggested a recessive (Abbie, '51). The data were submitted to Professor Catcheside for consideration. He agrees with the interpretation as a single gene mutation. He also calculated the gene frequencies in the 0–10 years group where the sexes and pigmentary distribution are almost equally represented (table 4). On the figures available he found the incidence of blondness equally consistent with either a dominant or a recessive, and therefore conclusive as to neither. More genealogical information is necessary to settle this point — the most extensive "tree" that could be compiled (fig. 3) has obvious deficiencies.

Leaving aside the question of dominance or recessiveness until more data are available, attention may be directed to the postulate of a single gene mutation. It is widely accepted that, in the general order of things, fairness as a whole is recessive to darkness as a whole (Davenport, '25; Cockayne, '33; Moore, '34; Trotter, '39; Gates, '48; Boyd, '50, and others), although several recognize that the problem is not so simple (e.g. Cockayne, '35; Keers, '35; Trotter, '39; Stern,

'49; Gates, '52). The present account of restricted blondness indicates that more factors are involved than the prevailing theory comprehends. The evidence available is inadequate for any extended consideration of this problem but it may be pointed out that there appears to be a close parallel in some cases of rutilism. Red hair is also classically considered recessive to dark but here, too, a single gene mutation appears to be an occasional cause and it may, apparently, manifest itself as a dominant (Keers, '33; Cockayne, '33; Moore, '34; Krogman, '36; Gates, '48). All this merely serves to illustrate the complexity of the mechanism of color inheritance, as does the incidence of some red pigmentation in the present series of aborigines. Campbell, Gray and Hackett ('36) incidentally, have noted two aboriginal beards with some red hair.

If this blondness is the result of single gene mutation, the further problem arises — is it ancient or recent? All the old accounts give the aborigine as dark haired or, where hair color is not mentioned, darkness is taken for granted. This may be only because the most considerable early contacts were on the east and south of the continent where blondness is sparse or absent. The earliest known account of fair hair dates from 1846–49 (see Carmichael, 1878). It is supplied by the first leader of the New Norcia Mission in Western Australia; he also records the same condition in a native from the eastern part of the continent. Matthew (1889) describes some blondness in northern New South Wales. Most other accounts (for references see beginning of article) relate almost entirely to Central and Western Australia although blondness is now known in Arnhem Land (C. P. Mountford, personal communication). The unexpectedness of the condition on the periphery of the continent is disclosed by the reaction of Mrs. Daisy Bates ('41) whose contact with the aborigines dates from about the beginning of the century. She attributed the southwestern blondness to the influence of two Dutch criminals marooned by Pelsart in 1627, and when she later encountered blond Central Australians who

had migrated south to Ooldea she suggested intermixture by members of the lost Leichhardt Expedition. However, no appeal to hybridization will serve and blondness in the Australian aborigine must be accepted as sui generis. This need occasion no special surprise since similar blondness has been reported in other, otherwise dark, peoples (e.g. by Sarasin, '25) and it may have occurred in the extinct Tasmanians (see Basedow, '25). Unfortunately, all this does not help to establish when blondness first appeared in the Australian aborigine and it seems that the best hope of reaching a solution to this problem rests upon an indirect approach, such as that initiated by Birdsell.

SUMMARY

1. The incidence of blondness is described in a group of over 100 Central Australian aborigines, mostly belonging to the same tribe.

2. This blondness affects only the hair of the head and the fine hair of the body. No other aspect of aboriginal pigmentation is involved.

3. The condition is most common in childhood. The hair darkens with age, more quickly and completely in males than in females.

4. The evidence suggests that this "particulate" blondness is due to a simple gene mutation, but whether dominant or recessive is uncertain.

5. It is not at present possible to estimate when the blond mutation first appeared.

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REVOLUTION VS. EVOLUTION: A PERSPECTIVE.— It could hardly be said today, as with some justice it might have been only a few years ago, that the platitudes of genetics are the heresies of anthropology. But in place of the violent revolution in anthropological thought which some great exponent of the genetic point of view might have stimulated, we are witnessing a slow and subtle infusion of genetic ideas suggesting one of those peaceful human infiltrations which have supplied anthropologists with many of their problems.— C. H. Danforth. Genetics and anthropology. Science, vol. 79, no. 2045, March 9, 1934, pp. 215–221.

One may properly maintain that the change now in progress from the older classical anthropology to human population genetics does in fact loom larger than gradual evolution; it stands at least as quantum evolution, and perhaps as a revolution.— J. B. Birdsell. On various levels of objectivity in genetical anthropology. This journal, vol. 10, no. 3, 1952, pp. 355–362.

THE CALIFORNIA INDIANS: A SOURCE BOOK. Compiled and edited by R. F. Heizer and M. A. Whipple. University of California Press, Berkeley, 1951. 487 pp., 15 pp.; 15 figs.; 12 maps. $6.50.— All but 4 of the 43 republished articles of this source book deal with archeology and ethnology. Two of these 4 are of sufficient interest to physical anthropologists to merit notice. The first is Kroeber's "Native Population of California," from two papers appearing in 1925 and 1939, which traces the dense (ca. 133,000) population of the 1760's to the 23,500 surviving claimants of Indian ancestry in 1928. The pre-1760 distribution of the population, combined with the increasing knowledge of aboriginal settlement patterns and the breeding units known through ethnological studies, should provide fair estimates of the size of breeding populations in aboriginal California. These estimates, in turn, should constitute an important part of the conceptual framework within which the living and skeletal data could be effectively analyzed. Second is Gifford's "California Indian physical types" (1926), a summary of his Californian anthropometry. It is still the only general article on the subject, although portions have been superseded; e.g., R. W. Newman (this journal, n.s. vol. 9, p. 237, 1951) demonstrated significant craniological changes in the Lower Sacramento sequence. Not superseded is Gifford's description of the physical variability of the living Indians, now too racially mixed except for two or three groups to merit restudy. Two of the three racial divisions Gifford established are far from convincing: The Californian type seems too composite a taxonomic category to be useful; and the Western Mono type represented by only 19 individuals needs validation. Thus only the concept of a Yuki type seems a useful one.— MARSHALL T. NEWMAN.

THE BLOOD GROUPS OF THE BUSHMEN

A. ZOUTENDYK, ADA C. KOPEĆ AND A. E. MOURANT

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The dark-skinned peoples who inhabit Africa south of the Sahara Desert clearly comprise a great many varieties of man, but two types have generally been regarded as standing out physically from the rest: the Pygmies of the Congo on the one hand, and the Bushmen and Hottentots of South Africa on the other. In some schemes of anthropological classification the Bushmen and the Negro have, indeed, been separated as major subdivisions of mankind.

Blood group evidence has not hitherto made such contribution to the problem of the relation between Bushmen and Negroes. Elsdon Dew ('39) has shown that the Bantu-speaking tribes of South Africa vary almost continuously from tribes with a high O frequency and only about 10% each of A and B genes to others with about 20% of A genes and 13% of B genes. The Bushmen were shown by Pijper ('32) to have on an average 20% of A and 7% of B genes, thus having more A and less B than most of the Bantu. The Hottentots, on the other hand (Pijper, '35), have a relatively high B frequency.

Recent work has greatly extended our knowledge of the distribution in Africa of the blood groups other than those of the ABO system, especially MNS and Rh. It therefore seemed desirable to obtain corresponding data for the Bushmen.

Short of embarking on a major expedition it was at first difficult to know how to set about collecting an adequate number of blood specimens from such a primitive, nomadic race, living in remote and inaccessible regions of Southwest Africa. The project was only made practicable by the enthusiastic co-operation of Dr. W. H. G. Kuschke, Regional Health Officer,

Runtu, S.W.A., without whose help and knowledge of the country and people it would have been impossible to begin the investigation. He collected the first 118 specimens of Bushmen blood either in venules or in sterile tubes; these were then transported to the base by road, and thence by air to Johannesburg. The remaining specimens were provided by Dr. Kuschke and by Dr. O. E. Budtz-Olsen whilst a member of a C.S.I.R. (South Africa) sponsored expedition to Southwest Africa under Professor J. F. Brock, of the Medical Faculty of the University of Cape Town.

The blood grouping tests were carried out at Johannesburg. All, or a substantial number, of the specimens were tested with the following sera: Anti-A, A_1, B, M, N, S, Henshaw, C, D, E, Lu^a, Kell, Le^a, Le^b, Fy^a.

All tests were carried out in tubes, centrifugation and microscopic confirmation of the results being resorted to where necessary. Slide tests were not employed.

ABO grouping. Every specimen was grouped on cells and serum at laboratory temperature.

Rhesus testing and typing. Tests with anti-C, anti-D and anti-E saline agglutinating sera were carried out on 232 specimens. All but two of these gave positive results with the anti-D serum used. These two exceptions gave negative results also with 5 other saline anti-D sera, and were also negative with anti-C and anti-E. They gave positive results, however, when tested with a strong "incomplete" anti-D serum by means of the indirect anti-globulin test of Coombs. The presence of the D^u antigen was thus demonstrated. A further 195 specimens were in the first place tested only with a saline anti-D serum, all but one giving positive results. This one also gave negative results with 5 other saline anti-D sera and with anti-C and anti-E, but was shown to contain the D^u antigen by means of an anti-globulin test with "incomplete" anti-D. There were thus shown to be no true D-negatives among the whole of the 427 Bushmen tested.

M, N, S, Henshaw and Lu^a. Tests were carried out at laboratory temperature with saline-agglutinating sera (human in the case of S and Lu^a, rabbit for M, N and Henshaw).

Kell. The specimens were tested by the indirect Coombs technique.

Duffy. With the exception of 17 specimens on which a saline agglutinating serum was used, the tests were carried out by the indirect Coombs technique.

Le^a and Le^b. As Lewis results are liable to be uncertain unless potent sera are used on fresh specimens of blood, tests were carried out at a laboratory temperature and confirmed at refrigerator temperature (6°C.). Owing to the relative weakness of the available anti-Le^a and Le^b sera when used for testing specimens of blood after a journey of several days, it was impossible to be confident of the results although fresh control specimens from known donors gave satisfactory reactions. We have, therefore, not quoted detailed results.

Sickle-cell trait. A search was also made for the sickle-cell trait. All the 118 specimens received from Dr. Kuschke for blood-grouping were tested, with negative results, by Dr. S. B. Griffiths who will give particulars of his investigations elsewhere (Griffiths, '53). Five hundred further samples were tested in the field also with negative results by Dr. O. E. Budtz-Olsen, who has kindly allowed us to quote his results in advance of publication in the detailed account of the expedition.

Gene frequency calculations were carried out by the methods which will be fully described by Mourant ('53). In the case of the ABO groups the method used is the correct method of Bernstein ('30). Wiener ('44) has shown that if only anti-C, anti-D and anti-E sera are used the problem of Rh gene frequencies can be reduced almost completely into terms of the ABO situation. We have therefore used an adaptation of Bernstein's corrected method for Rh frequencies. The results of these observations and calculations are set out in tables 1–7.

Our observed ABO frequencies agree closely with those found by Pijper ('32). The gene frequencies of the Bushmen fall just within the range of those found for Africans generally,

as shown by Elsdon Dew ('39, chart 8). The ABO results cannot at present be said to throw any important light on the relation between the Bushmen and other Africans.

The results of the MNS observations are similar to those found for most other African populations, which agree with

TABLE 1

The ABO blood groups of the Bushmen

GROUP	NUMBER OBSERVED	FREQUENCY OBSERVED	FREQUENCY EXPECTED	NUMBER EXPECTED
O	250	.5605	.5646	251.81
A	151	.3386	.3343	149.12
B	38	.0852	.0806	35.97
AB	7	.0157	.0204	9.10
Total	446	1.0000	.9999	446.00

Gene frequencies

A	.1967
B	.0519
O	.7514
	1.0000

TABLE 2

The MNS blood groups of the Bushmen

GROUP	NUMBER OBSERVED	FREQUENCY OBSERVED	FREQUENCY EXPECTED	NUMBER EXPECTED
MMS	14	.0745	.0752	14.13
MsMs	57	.3032	.2734	51.40
MNS	14	.0745	.0748	14.06
MsNs	66	.3511	.4088	76.86
NNS	3	.0160	.0149	2.81
NsNs	34	.1809	.1528	28.73
Total	188	1.0002	.9999	187.99

Chromosome frequencies

MS	.0675
Ms	.5229
NS	.0186
Ns	.3909
	.9999

one another and differ from most other known populations in having approximately equal frequencies of M and N genes with a low S frequency about equally divided between M and N, though usually with rather more MS than NS. The Bushmen have a rather high M frequency for Africa and a rather low NS frequency. The frequency of the Henshaw gene, 1.7%,

TABLE 3

The Henshaw blood groups of the Bushmen

PHENOTYPE	NUMBER	FREQUENCY
Henshaw-positive	4	.0333
Henshaw-negative	116	.9667
Total	120	1.0000

Frequency of He gene
.0168

MNS groups of Henshaw positives

MNS	2
NNS	1
NsNs	1

TABLE 4

The Rh blood groups of the Bushmen

PHENOTYPE	NUMBER OBSERVED	FREQUENCY OBSERVED	FREQUENCY EXPECTED	NUMBER EXPECTED
CDee	40	.1724	.1690	39.22
ccDee	181	.7802	.7835	181.77
ccD^{u}ee	2	.0086	.0087	2.01
ccDE	9	.0388	.0353	8.19
CDE	0	.0000	.0035	0.82
Total	232	1.0000	1.0000	232.01

Chromosome frequencies

CDe	.0904
cDE	.0196
cDe	.7970
cD^{u}e	.0930
	1.0000

TABLE 5

The Lutheran blood groups of the Bushmen

PHENOTYPE	NUMBER	FREQUENCY
Lu(a +)	0	0.00
Lu(a —)	89	1.00
Total	89	1.00

Gene frequencies

Lu^a	0.00
Lu^b	1.00
	1.00

TABLE 6

The Kell blood groups of the Bushmen

PHENOTYPE	NUMBER	FREQUENCY
K +	11	0.1038
K —	95	0.8962
Total	106	1.0000

Gene frequencies

K	0.0533
k	0.9467
	1.0000

TABLE 7

The Duffy blood groups of the Bushmen

PHENOTYPE	NUMBER	FREQUENCY
Fy(a +)	17	0.1574
Fy(a —)	91	0.8426
Total	108	1.0000

Gene frequencies

Fy^a	0.0821
Fy^b	0.9179
	1.0000

is of the same order as the 1.3% found in West Africa (Chalmers, Ikin and Mourant, '53). This gene is linked to the MNS system and has so far been found almost exclusively in Negroes. In them it is invariably accompanied by N and almost invariably by NS on the chromosome; it is therefore of great interest that the 4 Bushmen who are Henshaw-positive all have an N gene and three have an S gene, especially in view of the low total frequency of NS.

The Bushmen have one of the highest known frequencies of the cDe chromosome. All African populations south of the Sahara have a high frequency of this chromosome and all other known populations a low one. The chromosome $cD^{u}e$ is present with a frequency of 9%, but cde, which has a general African frequency of 20%, is absent.

Africans generally have a lower frequency of the Duffy (Fy^{a}) antigen than other tested races with the exception of the Brazilian Indians (Pantin and Junqueira, '51). In this the Bushmen agree with other Africans.

In view of the doubts mentioned above regarding the trustworthiness of our Lewis grouping results we have not quoted these in detail. It is however worth mentioning that we found an apparent very high frequency of the Le(a-b-) phenotype. Lawler and Barnicot ('53) have shown that this phenotype is more frequent among Africans than among Europeans.

In the absence of comparative data the Lutheran and Kell results are not at present of great anthropological significance.

In general, the Bushmen are found to agree to a remarkable extent with other African populations in their blood group frequencies, and especially to resemble or surpass them in all of those respects in which Africans generally differ from non-Africans. Perhaps of greatest interest is the very high frequency of cDe in the Bushmen, together with the absence of sickling. Following the discovery of high frequencies of sickling, with cDe infrequent or absent, in aboriginal Veddoid tribes of South India, Lehman and Cutbush ('52) have suggested that the sickle-cell trait entered Africa from Asia and had a separate origin from the high frequency of cDe, which

is the other most characteristic single genetical feature of Africans. They thus suggest the existence of a race with a high cDe frequency and no sickling as forming a major component of the population of Africa. The identification, in the Bushmen, of a population showing these features, lends strong support to the hypothesis of Lehman and Cutbush, especially as there are other grounds for regarding the Bushmen as being an ancient, well-differentiated people who once occupied a much larger area than they do at present. Before the hypothesis can be regarded as established, however, further surveys are needed in order to explore the relation between the frequencies of the Rh blood groups and of sickling throughout Africa, and perhaps in Asia as well.

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THE ABO, MNSs, P, Rh, LUTHERAN, KELL, LEWIS, DUFFY AND KIDD BLOOD GROUPS AND THE SECRETOR STATUS OF THE BLACKFOOT INDIANS OF ALBERTA, CANADA [1]

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Few blood group studies of Indians have been carried out in Canada, and those only for the ABO system.[2] In 1927 the MN and P systems were discovered; in 1939–40 the Rh system, and since then, 6 additional systems.[3] Over the past 7 years we have, in our spare time, and as blood-grouping sera became available to us, carried out studies of various Indian populations in Western Canada. These earlier studies, which are less complete than the present one, will be reported separately. With this experience behind us, and with the encouragement of Dr. F. J. Alcock and Dr. Douglas Leechman of the National Museum of Canada, it was decided to try to do a systematic survey of all blood groups of the

[1] We wish to acknowledge our debt to Dr. A. E. Mourant for several rare sera, to Dr. Sol Haberman for two of the anti-c sera, to Dr. P. Vogel for an anti-S serum and to Dr. W. T. J. Morgan for the anti-H used in the secretor tests on group O Indians.

[2] The tribes and numbers tested in each were (references in brackets): Beaver 40 (Grant, '36); Blackfoot 123, Piegan 42 (Matson, '38); Bloods 129 (Matson and Schrader, '33; Matson, '38); Chipewayan 69 (Grant, '33, '36); Cree 113 (Grant, '33; Matson, '38); Dogrib 77, Loucheux 28 (Grant, personal communication); Kwakiutl 275, Salish 50, Tsimshian 54 (Gates and Darby, '34); Micmac 279 (Gates, '38); Slave 79 (Gates, '29; Grant, '36); Stoney 207 (Grant, '36; Matson, '38).

[3] For information about the systems ABO, MNSs, P, Rh, Lewis, Lutheran, Kell, Duffy and Secretor, see Race and Sanger ('50); and about the Kidd system, see Allen et al. ('51) and Hunter et al. ('51).

Indians of Canada. The first of these studies under the aegis of the National Museum was carried out among the Canadian Blackfoot and Blood Indians in the summer of 1952.

THE INDIANS UNDER INVESTIGATION

The Blackfoot Indians of Canada consist of three tribes, the Blackfoot proper (population 1,250); the Bloods (population 2,002); the Piegans (population 730), each living in its own reserve in southern Alberta. Immediately to the south of the Blood Reserve is one in Montana, U.S.A., which is called the Blackfoot Reserve but whose population is largely Piegan. Long before the white man first made contact with these Indians 200 years ago, the three tribes formed an insoluble confederacy, claiming control of a vast area extending from the North Saskatchewan River to the upper Missouri and from the Rocky Mountains east across the plains into the present Province of Saskatchewan. According to Linderman ('47) "the three tribes are one people. They speak a common language and practice the same customs. Long ago [they] were a timber people inhabiting the forests near Lesser Slave Lake. Incessant warfare pushed them southward." There is some doubt about this early history, but at their entrance into written history they were nomadic horsemen, numbering perhaps 10,000, proud and warlike. There was said to be no intermarriage with other tribes, though it seems altogether likely that women captured in warfare would be eventually absorbed into the tribe. There definitely was intermarriage between members of the three tribes of the confederacy. With the coming of the Whites miscegenation began, although it is only from about 1850 on that first traders, and later settlers, came into the territory in numbers. In addition to interbreeding with Whites, at least the Blackfoot tribe accepted into its membership some Plains Crees. In our sample of "Blackfoot" 4 are known to have a Cree ancestor. A detailed sociological study of the Blackfoot tribe has been made by Hanks and Hanks ('50).

With the Whites came their diseases. Smallpox, tuberculosis and other infections reduced the Indian population by at least half. In the 1880's with the coming of the railroads and white settlements and with the disappearance of the buffalo which had served these Indians as their source of food, clothing and building materials, the remnants of the tribes in Canada were, by treaty, confined to their present reserves. At that time their populations were estimated at Blackfoot 197 families; Blood 546 families; Piegans 193 families. Family size was not estimated, but since living conditions at that time were bad, with a high infant mortality, the families were probably small. Multiplying these family figures by 4 gives a close approximation to the present population of the Blood and Piegan tribes but only about half the present population of the Blackfoot. As stated above the Blackfoot accepted into its membership some Plains Crees, but we have not been able to find out how many. As later pointed out in the data on the MNS blood group, this possibly large mixture may be evidenced in our gene determination.

Even after the Indians were confined to their reserves, malnutrition and disease continued to reduce their numbers, until it was thought they might disappear. Today their conditions of life have improved a great deal; many are successful farmers and cattlemen under the guidance of outstanding Indian Agents; the Indian Health Services are doing an excellent and much appreciated work both in preventive and curative medicine. The net annual population increase is nearly 3%.

In the summer of 1952 we spent one week on the Blackfoot Reserve and 4 weeks on the Blood Reserve. In the former, through the kind cooperation of the Reverend Mr. Cole, Superintendent of Old Sun School, and Mr. W. Pugh, Indian Agent on the Reserve, we tested 39 children between the ages of 7 and 16 years. In the latter, we tested 241 individuals for the purpose of the present study, as well as several additional families to follow the inheritance of certain factors. We do

not make use of the latter in the present study, but will report the data collected in a separate paper.

On the Blood Reserve we were extremely fortunate in obtaining, through the good offices of Mr. G. H. Gooderham, Inspector of Agencies, and Mr. R. D. Ragan, Indian Agent, the services of Chief Percy Creighton as our interpreter. The Indians themselves were most generous and cooperative, and yet without Chief Creighton's assistance we could have made little progress. He was particularly valuable in his knowledge of the interrelationships of individuals and families and of genealogies going back two or three generations.

Through the cooperation of Dr. Lynne Falconer, Director of Indian Medical Services, a field laboratory was set up at the Indian Hospital on the Blood Reserve. This included a small portable refrigerator which we had taken with us and which allowed us to keep liquid or reconstituted dried sera frozen between tests. About 20 blood samples and saliva samples were collected on the Reserve each morning, and tested that afternoon and evening. Where indicated blood specimens were saved in the refrigerator for recheck the following day. The A, B, and AB salivas were tested the day they were collected. The O salivas were heated and then refrigerated until we were leaving the Reserve, when they were sent by air to our laboratory in Winnipeg and kept frozen until our return.

RESULTS

The results are given in the order in which the blood groups were discovered.

The ABO blood group system. The results are set out in table 1. These are in good agreement with the earlier studies of the tribes of the confederacy, which proved that they have a higher frequency of gene A than any other people so far reported.

The MNSs system. The results are set out in tables 2, 3, 4 and 5. It will be seen that the two population samples do not agree in their MN distribution (table 2) but do agree in

TABLE 1

The A–B–O system

	NUMBER					PER CENT OF GROUP				GENE FREQUENCIES			D	σD	D/σD	χ^2	P
	Total	*O*	A_1	*B*	A_1B	*O*	A_1	*B*	A_1B	A_1	*B*	*O*					
Blood	241	40	196	2	3	16.60	81.33	0.83	1.24	.5824	.0104	.4072	—.0003	.0055	—.055	.00	1
Blackfoot	39	6	33	0	0	15.38	84.62	0.00	0.00	.6078	.0000	.3922	.0000	.0801	.000	.00	

$\chi^2 = 0.24$.

For the two populations the hypothesis is that they do not differ significantly in gene frequencies. For each blood group system this hypothesis is tested by estimation of chi-square, which is recorded under each table. Only in the case of the MN system is there a real discrepancy; for the other systems there is no reason to doubt the hypothesis.

The statitsical tests to the right of tables 1 and 2 are estimates of internal consistency, which we judge to be present. The frequencies given of genes A, B and O were determined by Bernstein's improved method, whereas the statistical tests are of the frequencies determined by his original method. See Race and Sanger ('51).

TABLE 2

The M N–S–s system: M–N frequencies

TRIBE	NUMBER				PERCENTAGE FREQUENCIES			GENE FREQUENCIES		D	σD	D/σD	χ^2	P
	Total	*M*	*MN*	*N*	*M*	*MN*	*N*	*M*	*N*					
Blood	241	181	59	1	75.10	24.48	0.42	.8734	.1266	.0686	.0322	2.13	2.77	.10
Blackfoot	39	19	19	1	48.72	48.72	2.56	.7308	.2692	.1420	.0801	1.78	2.21	.15

$\chi^2 = 12.52$.

TABLE 3

The M N-S-s system: S-s frequencies

TRIBE	NUMBER			PERCENTAGE FREQUENCY		GENE FREQUENCY	
	Total	*S* +	*S* −	*S* +	*S* −	*S*	*s*
Blood	241	149	92	61.83	38.17	.3822	.6178
Blackfoot	39	23	16	58.97	41.03	.3595	.6405

$\chi^2 = 0.12$.

TABLE 4

The M–N–S–s system

	NUMBER						PERCENTAGE FREQUENCIES						GENE FREQUENCIES			
	MM.S	*MsMs*	*MN.S*	*MsNs*	*NN.S*	*NsNs*	*MM.S*	*MsMs*	*MN.S*	*MsNs*	*NN.S*	*NsNs*	*MS*	*Ms*	*NS*	*Ns*
Blood	104	77	45	14	0	1	43.15	31.95	18.67	5.81	0.00	0.42	.3014	.5652	.0686	.0648
Blackfoot	9	10	13	6	1	0	Not calculated.									

their Ss (table 3), while there is good agreement within the sample of Blood Indians between the expected and observed MNSs phenotype frequencies (table 5). The disagreement in table 2 may be real, the two tribes actually differing in their MN gene frequencies, or it may be only apparent. When the two sets of data are examined for evidence of internal consistency they both appear statistically consistent. Both samples were tested with the same sera and by the same methods. Two explanations for the disagreement offer themselves to

TABLE 5

The M–N–S–s system

The expected and observed phenotype frequencies in the Bloods

	PER CENT		ABSOLUTE NUMBERS		χ^2
	Expected	Observed	Expected	Observed	
MMS	.4315	.4315	103.99	104	.00
MMs	.3195	.3195	77.00	77	.00
MNS	.1579	.1867	38.05	45	1.23
MNs	.0732	.0581	17.64	14	.75
NNS	.0136	.0000	3.28	0	3.28
NNs	.0042	.0042	1.01	1	.00
	.9999	1.0000	240.97	241	5.26; $n = 2$; $p = .10 > p > .05$

Since no NN.S individual was observed, the gene frequency for NS was estimated by subtracting the calculated gene frequencies from 1. The expected phenotype frequencies are derived on this basis. Some discrepancy may well be expected in the phenotypes containing NS.

us: the small size of the Blackfoot sample, or an unrecognized intermixture with Plains Cree Indians in this sample (see above). A larger sample should be studied, and the genealogy of those making up the sample determined.

The P system. The anti-P serum which we used was from one of our own patients. While, under the conditions of our home laboratory, this gave clear-cut results, under the high pressure conditions of the field, where 400 or more tests with different sera and by different methods were being carried out of an afternoon and evening, we had much difficulty in deciding between very weak positive and negative reac-

tions. We can say that about 85% of the Indians were P-positive. Wiener et al. ('45) reported 78.9% of 95 Mexican Indians to be P-positive. We know of no other published report of the P system in Indians.

TABLE 6

The Rh system

TRIBE	NUMBER									
	Total no.	R_1R_2 *ccDEe*	R_1R_1 *CCDee*	R_1r *CcDee*	R_2R_2 *ccDEE*	R_2r *ccDEe*	R_1R_z *CCDEe*	R_2R_z *CcDEE*	*rr ccddee*	$R''r$ *ccddEe*
Blood	241	100	53	20	31	20	9	6	1	1
Blackfoot	39	19	9	2	8	1	0	0	0	0

TRIBE	PERCENTAGE FREQUENCY									
	Total no.	R_1R_2	R_1R_1	R_1r	R_2R_2	R_2r	R_1R_z	R_2R_z	rr	$R''r$
Blood	241	41.49	21.99	8.30	12.86	8.30	3.73	2.49	.42	.42
Blackfoot	39	48.72	23.08	5.13	20.51	2.56	..	..	..	..

TRIBE	GENE FREQUENCIES				
	R_1	R_2	R_z	R''	r
Blood	.4689	.4011	.0383	.0269	.0648
Blackfoot	Not estimated.				

When the Blackfoot were being studied only a single anti-c serum was used. This later turned out to contain anti-E as well as anti-c. The R_1R_z would therefore react with this serum and appear to be R_1R_2. The gene frequencies of the Blackfoot were not estimated, both for this reason and because the numbers are small. The gene frequencies of the Bloods were used in estimating both their own genotype and phenotype frequencies and the phenotypes of the Blackfoot.

The Rh system. The results are set out in tables 6, 7 and 8. Anti-C, anti-c, anti-C^w, anti-D, anti-E and anti-e sera were used. Actually we had for use 3 pure anti-C, 3 anti-C + C^w, 2 anti-C^w, 6 anti-c, 3 anti-D, 2 anti-E and 1 anti-e. When weak or doubtful reactions occurred the blood was checked with further sera of the same specificity (except anti-e, of course). Unfortunately the sample of Blackfoot was tested for the

antigen c with only one strong anti-c serum, which later proved to contain anti-E also.[4]

One Blood Indian, with a White ancestor, was of genotype $C^wDe.cde$. This has been included with CDe.cde in our analysis. The cde.cde and cdE.cde bloods were checked for D^u. It was not present.

TABLE 7

The Rh system

The expected genotype and the expected and observed phenotype frequencies in the Bloods

GENOTYPES		PHENOTYPES			χ^2
Name	Expected frequencies	Expected frequencies	Absolute number		
			Expected	Observed	
R_1R_2	.3761	.4063	97.92	100	0.04
R_zr	.0050				
R_1R''	.0252				
R_1R_1	.2199	.2199	53.00	53	0.00
R_1r	.0607	.0607	14.63	20	1.97
R_2R_2	.1609	.1825	43.98	31	3.83
R_2R''	.0216				
R_2r	.0520	.0520	12.53	20	4.45
R_1R_z	.0359	.0359	8.65	9	0.01
$R''R_z$	.0021	.0328	7.90	6	0.46
R_2R_z	.0307				
$R''r$	.0035	(The rest) .0099	2.39	2	0.06
rr	.0042				
R_zR_z	.0015				
$R''R''$	.0007				
	1.0000		241	241	10.82; n = 7; $.10 < p < .20$

[4] Dr. R. R. Race and Dr. Ruth Sanger suggested that two of our anti-c sera contained anti-E. This proved correct. We are most grateful to them for this suggestion. About half of the anti-c sera that we have or have had in the past, as judged by their reactions with the blood of R_1R_z Indians of various tribes, have apparently contained anti-E. This source of error is drawn to the attention of other investigators. The anti-c + E sera were not used in the tests on the Blood Indians.

In the Indians recorded in the tables only genes CDe (R_1), cDE (R_2), cde (r) and cdE (R'') were identified. CDE (R_z) is assumed in preference to CdE (R_y) because, in other studies of Indians of Western Canada, we have by family studies proved the existence of R_z but not of R_y. Some families that contained phenotypes R_1r or R_2r were followed through two or more generations to try to prove whether the gene cDe (R_0) was present. These families, beyond the propositus, are not included in the present data. Gene cDe could not be proven to be present. The statistical analyses

TABLE 8

The Rh system

The expected and observed frequencies in the Blackfoot based on the gene frequencies of the Bloods

PHENOTYPES				
Name	Expected frequency	Absolute number		χ^2
		Expected	Observed	
R_1R_2	.4422	17.24	19	0.20
R_1R_1	.2199	8.58	9	0.02
R_1r	.0607	2.37	2	0.06
R_2R_2	.1825	7.12	8	0.11
R_2r	.0520	2.03	1	0.52
The rest	.0427	1.66	0	1.66
	1.0000	39.00	39	2.58; n = 5; $.70 < p < .80$

of our results based on the above 5 genes are compatible with the hypothesis that only these 5 exist in the population samples examined.

The Lutheran system. Of the Blood Indians 97 were tested with anti-Lu^a. All were negative, so that the assumption is that the population sample is homozygous Lu^bLu^b.

The Kell system. Thirty-nine Blackfoot and 241 Bloods were tested with anti-K. All were negative. Only a few were tested with anti-k because we have found that Indians who are K-negative are k-positive just as are Whites. We assume the population to be homozygous kk.

The Lewis system and the Secretor system. Thirty-nine Blackfoot and 241 Bloods were tested with anti-Le^a. All were negative. The same bloods were tested with an anti-Le^b cold agglutinin, and while the great majority gave a sharp reaction others were doubtful, so that we do not feel we can set down an exact percentage of reactors.

The gene Sec (Secretor) is closely associated with gene Le^b. Of the Blood Indians 210 of groups A, B and AB and 31 of group O were tested for the ability to secrete. All the

TABLE 9

The Duffy system

TRIBE	NUMBER			PERCENTAGE FREQUENCY		GENE FREQUENCY	
	Total	*Fy(a+)*	*Fy(a−)*	*Fy(a+)*	*Fy(a−)*	Fy^a	Fy^b
Blood	235	220	15	93.62	6.38	.7474	.2526
Blackfoot	39	38	1	97.44	2.56	.8400	.1600

$\chi^2 = 0.89$.

TABLE 10

The Kidd system

TRIBE	NUMBER			PERCENTAGE FREQUENCY		GENE FREQUENCY	
	Total	*Jk(a+)*	*Jk(a−)*	*Jk(a+)*	*Jk(a−)*	Jk^a	Jk^b
Blood	194	179	15	92.27	7.73	.7220	.2780
Blackfoot	39	34	5	87.18	12.82	.6419	.3581

$\chi^2 = 1.07$.

A, B and AB and 30 of the 31 O were secretors. This is a percentage frequency for secretor of 99.5851, and for non-secretor of 0.4149, with gene frequencies of Sec .9356 and sec .0644. With such a distribution this can only be an approximation, but it does appear that the gene frequency of both Sec and Le^b is very high, of sec and Le^a correspondingly low.

The Duffy system. The results are set out in table 9. Only anti-Fy^a was available for testing.

The Kidd system. The results are set out in table 10. Only anti-Jk^a was available for testing.

DISCUSSION

It will be seen that, except in the case of genes M and N there is close agreement between the frequencies of the genes tested for in the two tribes. Indeed there is closer agreement than one might reasonably hope for, using two samples the size of these from a single small population. The question of the MN frequencies of the Blackfoot requires further study.

It is hardly necessary to point out that one is not justified in generalizing from the present particular investigation. The gene frequencies found apply to these tribes and not to American Indians at large. The gene frequencies of other tribes can be determined only by actual tests. After this has been done over large areas of the Americas we may then be able to say with some certainty what the genetic relationships are of tribe to tribe and what the origins of the American Indians were.

There do, however, appear to be two well substantiated facts about the blood groups of the Indians at large. First, the gene B does not occur in purebred Indians of North America, and second, gene cde does not occur in purebred Indians in North or South America. If this be true then the ratio between the frequency of these genes in the Indian population and their frequency in a White population should suggest the approximate percentage of originally White genes in any system. For both B and cde this works out in the present case to roughly at one-sixth, as deduced from our own data on Whites (Chown et al., '49). From this it is a simple matter to calculate the approximate gene frequencies of the Blood Indians prior to interbreeding with Whites. The results of such calculations are set out in table 11.

SUMMARY

The 9 blood group systems and the secretor system of the Blood and Blackfoot Indians were studied. These Indians are known to have some White blood. The gene frequencies for all but the P and Lewis systems are summarized in table 12. The

results were examined where possible for internal consistency and in all cases to test the hypothesis that the two samples did not differ statistically in their gene frequencies. There appeared to be internal consistency. No reason was found

TABLE 11

Hypothetical gene frequencies of pure-blood Indians of the Blood tribe

Calculated from the deduction that 1/6 of the present genes are of White origin

GENETIC SYSTEM	HYPOTHETICAL GENE FREQUENCY			
Lutheran	Lu^a	.00	Lu^b	1.00
Kell	*K*	.00	*k*	1.00
Secretor	*sec*	.00	*Sec*	1.00
Lewis	Le^a	.00?	*Not* Le^a	1.00 [1]
P	*P* —	.00?	*P* +	1.00?
D–d (Rh)	*d*	.03	*D*	.97
M–N	*N*	.06	*M*	.94
Duffy	Fy^b	.18	Fy^a	.82
Kidd	Jk^b	.23	Jk^a	.77
A–B–O	*O*	.36	*A*	.64
S–s	*S*	.38	*s*	.62
E–e (Rh)	*e*	.48	*E*	.52
C–c (Rh)	*c*	.48	*C*	.52
Rh chromosomes	$R_1 - R'$		.48 – .00	
	$R_2 - R''$		.45 – .03	
	$R_Z - R_Y$		.04 – .00	
	$R_0 - r$		.00 – .00	
MNSs chromosomes	$MS - Ms$		.31 – .61	
	$NS - Ns$		.07 – .01	

[1] In the Indians tested, one out of 241 was Le(a —) and a non-secretor. This individual must then be either genotype Le(a — b —) or genotype Le(a — b +). If Sec is absolutely linked to Le^b the former would be the true genotype. In the absence of further information we cannot be certain whether the Lewis alleles of this population are Le^a and Le^b, or Le^a, Le^b and one or more others. The allele of Le^a is therefore shown as "not Le^a."

in the data to doubt the hypothesis except in the MN distribution. The latter discrepancy may be due to the small size of the sample of Blackfoot or to interbreeding between Blackfoot and Plains Crees.

Gene frequencies could not be determined in the P and Lewis systems. It was estimated that both samples are about

TABLE 12

Summarized results

GENETIC SYSTEM	GENE	BLOOD		BLACKFOOT	
		Gene freq.	No. tested	Gene freq.	No. tested
A–B–O	*A*	.5824	241	.6078	39
	B	.0104		.0000	
	O	.4072		.3922	
M–N	*M*	.8734	241	.7308	39
	N	.1266		.2692	
S–s	*S*	.3822	241	.3595	39
	(s)	(.6178)		(.6405)	
D–d (Rh)	*D*	.9083	241		
	(d)	(.0917)			
C–c (Rh)	*C*	.5072	241		
	c	.4928			
E–e (Rh)	*E*	.4663	241		
	e	.5337			
Lutheran	Lu^a	.0000	97		
	(Lu^b)	(1.0000)			
Kell	*K*	.0000	241	.0000	39
	(k)	(1.0000)		(1.0000)	
Secretor	*Sec*	.9356	241		
	sec	.0644			
Duffy	Fy^a	.7474	235	.8400	39
	(Fy^b)	(.2526)		(.1600)	
Kidd	Jk^a	.7220	194	.6419	39
	(Jk^b)	(.2780)		(.3581)	

		BLOOD
Rh chromosomes	*CDe – Cde*	.4689 – .0000
	cDE – cdE	.4011 – .0269
	CDE – CdE	.0383 – .0000
	cDe – cde	.0000 – .0648
MNSs chromosomes	*MS – Ms*	.3014 – .5652
	NS – Ns	.0686 – .0648

The brackets mean that the antigen governed by this gene was not tested for directly, i.e., the sera anti-s, d, Lu^b, Fy^b and Jk^b were not used. Anti-k was used on a small number to satisfy ourselves that K-negative Indians are k-positive, as has always proven true in a great many other cases.

85% P-positive. All 39 Blackfoot and 241 Bloods were Le^a-negative. A high percentage of both were Le^b-positive.

From the ratio of the frequency of genes B and cde between the Bloods and a White population it was estimated that about one-sixth of the genes of the present population derive from Whites. On this basis the hypothetical gene frequencies for purebred Indians of the Blood tribe were calculated.

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LETTER TO THE EDITOR.— The March, 1953, issue of the *Journal* contains an article by Pantin and Kallsen entitled, "The Blood Groups of the Diegueño Indians." Mention is made of visits to 9 specific reservations and the impression is given that all of these reservations belong to "Pima-speaking" Diegueño Indians. This is not the case.

The Indians on the reservations at Rincon, La Jolla (near Palomar Mountain), and Pauma are Luiseños who speak a Shoshonean language belonging to the Uto-Aztecan stock. As for the Indians at Pala, they are, for the most part, Cupeños who speak a similar tongue; the remainder are largely Luiseños and Cahuillas, and only a few are Diegueños. Finally, the Los Coyotes reservation belongs to the Shoshonean-speaking Mountain Cahuilla, with some Cupeño elements.

Only Mesa Grande, Capitan Grande, Inaja, and Santa Ysabel are Diegueño reservations, although the last-named contains a strong Cupeño element. Incidentally, it is wrong to speak of the Diegueños as Pima-speaking. The Pima of Arizona and the Diegueño of California speak related languages, but the latter employ a Yuman language of the Hokan stock and not a Pima one.

For the sake of accuracy the article might better have been labelled, "The Blood Groups of Some San Diego County Indians and Part-Indians."

WILLIAM A. LESSA

COMPARISON OF GENETICAL AND MORPHOLOGICAL METHODS FOR A STUDY OF BIOLOGICAL DIFFERENCES [1]

L. D. SANGHVI [2]
MORPHOLOGICAL DATA COLLECTED BY G. M. KURULKAR
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TWO FIGURES

Man has always been interested in classifications. Observation of differences, real or imaginary, is the basis of all such classifications. Classifications of man himself, like the ones prevalent in prehistoric India, in ancient Greece or even in contemporary Europe, were largely based on cultural differences (linguistic, religious, national), giving rise to group-feelings; and the problems concerned with such classifications belong to the field of social psychology.

[1] Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Columbia University.

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Comparatively more recent are the classifications of the living world, including man himself, based on biological differences. These were first given shape by Linnaeus. Since Darwin's synthesis of organic evolution, observations on the biological differences among different groups of organisms have taken a special significance. They have ceased to be of a static nature, and have assumed a dynamic significance to take into account variations, differentiations and fusions of such groups.

Morphological methods have been in great use for describing these biological differences among organisms including man. With the advent of genetics, frequency of genes and phenotypes of the genetically determined traits have also been used for describing biological differences.

Studies of biological differences based on characters with known effects for natural selection would be desirable for an understanding of the dynamic aspects of such differences. Our knowledge of the effect of natural selection on biological characters in man is, however, woefully inadequate.

One of the elementary processes of organic evolution is variation in gene-frequency. Characters with a known mechanism of heredity have an advantage for studying the factors involved. The exact mode of heredity of most of the morphological characters is not known, which puts a limitation on their use for studying these factors. On the other hand, the most direct evidence of organic evolution comes from fossil material. At present, very little genetical information might be obtained from such material, although comparative morphological studies can easily be made.

An essential step in advancing our knowledge, at present, of biological differences would seem to be a comparison and evaluation of the two chief biological methods, which may be called the morphological method and the gene-frequency or the genetical method. For a study of certain basic biological problems, man has not been a particularly suitable organism. On the other hand, for a study of intergroup differences, more material is available for man than for any other organ-

ism, if full account is taken of morphology, genetics and breeding structure. The material provided by the endogamous groups in India seems especially favorable for studying these questions.

The people of India are broken up into a large number of endogamous groups (or Mendelian populations; Dobzhansky, '51), whose members are forbidden by social law to marry outside their own group. These endogamous groups form the framework of the social organization known as the caste system. The caste system is theoretically restricted to the Hindu community,[4] but the influence of endogamy has penetrated the barriers of Islam and even Christianity. These groups have a general resemblance in the practices they observe and the mechanism by which they are maintained; but they are vastly different in their names, numbers, characters and social functions. The origin and evolution of a large majority of these groups are lost in a distant past which critical history cannot trace. Some of these groups have remained socially isolated for a hundred generations or more.

There is a custom almost universal among these endogamous groups, which breaks each one of them into mutually exclusive sections, whose members are forbidden to marry within their own sections. There is no parallel of this type of exogamy in Western society; it would mean more or less that a Mr. Smith cannot marry a Miss Smith but has to marry a non-Smith, say a Miss Brown. An exogamous section derives its name from some mythical ancestor from whom all the members of that section are supposed to have descended in the male line. These exogamous sections, like the endogamous groups, vary widely in their limits, titles and definitions.

Investigations concerning the morphological measurements of the people of India were begun during the latter half of

[4] The word "Community" has a special meaning in India. It refers to a religious group, to distinguish it from a caste, which may consist of one endogamous group or several such groups. Out of a total population of 318,776,000 of India (census of '51) 75.09% belonged to the Hindu community, 13.39% to the Moslem community, 7.78% to various tribes, and the 3.74% of the population was divided among Christians, Sikhs, Jains, Buddhists, Parsees and Jews.

the last century. Comprehensive studies on the subject were undertaken by Risley ('15) and Guha ('31, '37), both of whom studied a large number of individuals comprising several different groups.

Investigations concerning the genetical traits have been few and far between in India compared with some other countries of the world. Preliminary studies carried out at the Tata Memorial Hospital, Bombay, revealed striking genetical differences between different endogamous groups and suggested that it might be of interest to examine several endogamous groups both for genetical traits and for morphological measurements, and to compare the biological differences between these groups based on the genetical and morphological methods.

GENETICAL AND MORPHOLOGICAL DATA

The following 5 endogamous groups whose members were available in Bombay and vicinity were selected in the present study:

ENDOGAMOUS GROUP	ABBREVIATION
Vadnagarā Nāgar Brāhman (Suddha)	V.N.B.
Desasth Rigvedi Brāhman	D.R.B.
Desasth Yajurvedi Brāhman (Sukla)	D.Y.B.
Koknasth Brāhman (or Chitpāvan)	K.B.
Chāndraseniya Kāyasth Prabhu	C.K.P.

A caste is either a single endogamous group or a collection of several such groups. The caste of C.K.P. is a single endogamous group. On the other hand, the caste of Brāhmans numbering 1,052,978 in the same area (census of '01) comprises a large number of such groups. It is primarily divided into geographical groups (1) Gurjar, (2) Mahārāshtra, (3) Sārasvat and (4) Karnātak. Gurjar Brāhman consists of 93 divisions. One such division called Nāgar, has 6 subdivisions. One of the subdivisions called Vadnagarā has 4 further divisions, viz. Suddha, Bhiksuk, Dungarpurā and Bārad.

Desasth and Koknasth are two divisions of Mahārāshtra Brāhmans. Koknasth Brāhman forms a single endogamous group. Desasth is subdivided into (1) Rigvedi and (2) Yajurvedi. Rigvedi forms a single endogamous group while Yajurvedi is further divided into (1) Sukla and (2) Krsna. One of the subdivisions called Mādhyāndin of Sukla Yajurvedi was selected for the present study.

Of these 5 endogamous groups, V.N.B. is a Gujarati speaking group and the other 4 are Marāthi speaking. All of these groups practice exogamy within the caste. There are 15 exogamous sections (gotras) in K.B. and 24 in C.K.P. There are, however, differences in the consanguineous marriage customs among these groups. No marriage between a boy and his maternal uncle's daughter (cross-cousin marriage) is permitted in V.N.B., K.B. and D.Y.B., whereas among D.R.B. and C.K.P. not only is this practice prescribed by social custom, but an extravagant weight is put on it.

Demographic information on these endogamous groups is scanty and has a varying degree of accuracy. Decennial census figures are available from 1881 onwards, but the information about the endogamous groups is not reported in all. Special efforts were made by census commissioners in 1901 and 1931 to secure greater accuracy in the data of the endogamous groups. Numerical strength of the endogamous groups under study from these census tables is shown below.

ENDOGAMOUS GROUP	1901	1931
V.N.B.	21,617	6,611 (sic)
D.B.	155,305	302,530
K.B.	113,605	119,611
C.K.P.	21,941	31,126

Separate figures for D.R.B. and D.Y.B. are not reported. D.B. represents all Desasth Brāhmans. In Bombay State, V.N.B. and C.K.P. are concentrated in the northern region, and D.B. in the southern regions, while K.B. is distributed in the central as well as southern regions.

Genetical data. The genetical data consist of ABO, MN and Rh blood groups, taste reactions to phenyl-thio-carbamide and color-blindness of the red-green type, examined for 100 adult men (age range 20–55) from each of the 5 endogamous groups. All the individuals examined were available in Bombay. Table 1 contains a summary of these data. Detailed techniques and the data *in extenso* are already published elsewhere (Sanghvi and Khanolkar, '49). The notations used for genetical traits and phenotypes are given below.

Blood group OAB	O, A, B, AB
Blood group MN	M, N, MN
Blood group Rh	Rh-Positive = +; Rh-Negative = —
Taste reaction to p.t.c.	Taster = +; Non-Taster = —; doubtful = ?
Color vision c.v.	Normal = +; red-green blind = —

Morphological data. A request was made to Dr. G. M. Kurulkar of Seth G. S. Medical College, Bombay, to collect the morphological data for these groups. Doctor Kurulkar kindly consented, and has taken 11 measurements of head and face on all 500 men, following the methods advocated by Hrdlička and Martin. Table 2 contains a summary of his data along with his calculations.

STATISTICAL ANALYSIS

The genetical and morphological data reported above for the endogamous groups give individually the biological information for each group. Simple statistical tests are available for arriving at the significance of a single character, either genetical or morphological, between a pair of endogamous groups. χ^2-test gives the significance for the genetical traits and the t-test gives the significance for the morphological measurements. It was, however, found necessary to have statistical methods by which it would be possible to arrive at a quantitative measure of biological difference between a pair of endogamous groups based on *all the characters,* either genetical or morphological, studied for these groups. Such a quantitative measure based on genetical traits may be, for the sake of convenience, called a genetical difference and the

TABLE 1

Genetical data of the five endogamous groups in Bombay

ENDOGAMOUS GROUP	NO. OF PERSONS	GENETICAL CHARACTER														
		ABO				MN			Rh		p.t.c.			Color vision	
		O	A	B	AB	M	N	MN	+	—	+	—	?	+	—
V.N.B.	100	41	30	25	4	46	9	45	91	9	71	28	1	90	10
D.R.B.	100	37	28	29	6	33	18	49	93	7	62	36	2	97	3
D.Y.B.	100	38	22	31	9	35	14	51	97	3	65	33	2	97	3
K.B.	100	51	25	20	4	41	11	48	97	3	65	32	3	95	5
C.K.P.	100	35	30	26	9	33	19	48	91	9	55	45	..	99	1

TABLE 2

Morphological data of the five endogamous groups in Bombay (Kurulkar). Mean measurements and standard errors expressed in millimeters

MORPHOLOGICAL MEASUREMENTS	ENDOGAMOUS GROUP				
	V.N.B.	D.R.B.	D.Y.B.	K.B.	C.K.B.
1. Head length	187.2 ± 0.6	187.2 ± 0.7	185.6 ± 0.6	189.5 ± 0.6	185.6 ± 0.7
2. Head breadth	150.7 ± 0.5	144.1 ± 0.6	142.7 ± 0.5	145.4 ± 0.5	144.6 ± 0.6
3. Minimum frontal breadth	106.3 ± 0.5	105.0 ± 0.4	105.1 ± 0.5	105.4 ± 0.5	104.0 ± 0.4
4. Bizygomatic breadth	136.3 ± 0.6	134.3 ± 0.5	134.0 ± 0.5	135.4 ± 0.4	132.3 ± 0.5
5. Bigonial breadth	95.7 ± 0.7	95.1 ± 0.6	97.7 ± 0.7	94.9 ± 0.6	93.6 ± 0.5
6. Total facial height	113.9 ± 0.7	113.5 ± 0.5	114.2 ± 0.6	114.2 ± 0.6	114.4 ± 0.6
7. Upper facial height	62.5 ± 0.4	61.3 ± 0.4	60.7 ± 0.4	61.8 ± 0.4	60.5 ± 0.4
8. Nasal length	52.0 ± 0.4	52.0 ± 0.3	50.7 ± 0.3	50.7 ± 0.4	51.3 ± 0.3
9. Nasal breadth	35.9 ± 0.2	38.6 ± 0.3	37.4 ± 0.3	38.1 ± 0.3	36.9 ± 0.3
10. Biorbital breadth	92.9 ± 0.4	91.7 ± 0.4	91.1 ± 0.4	93.1 ± 0.3	90.3 ± 0.4
11. Interorbital breadth	32.1 ± 0.2	32.1 ± 0.3	32.4 ± 0.3	31.1 ± 0.3	30.7 ± 0.2
Number of persons	100	100	100	100	100

one based on the morphological measurements may be called a morphological difference. Values of genetical and morphological differences for all possible pairs of endogamous groups would make it possible to understand the relationship between the groups and compare the relationship based on genetical differences with the one based on morphological ones.

Mahalanobis ('36) has devised an appropriate statistical method for arriving at a quantitative measure of biological difference based on morphological measurements. He has called this measure of difference the "generalized distance." Very considerable labor is involved in calculating this function, particularly when the number of measurements is large. Rao ('48) has suggested some short cuts in the computation, but it still remains formidable. For the present study, a simple property of the t values was used to arrive at a measure of differences based on the morphological measurements.

In order to compare the use of morphological and genetical differences it was necessary to devise a quantitative measure of biological differences based on discrete characters like the genetical ones. Two different methods were considered for this purpose: one, based on the probability of correct classification of a single individual by the minimax solution (Rao, '48; Wald, '50) and the other, based on the cumulative nature of χ^2 values. There is a close correspondence between the two methods. The χ^2 method is, however, more appropriate for the range of values that are important from an evolutionary point of view. It is also simpler to compute. This method is described below.

Genetical differences

Table 3 contains χ^2 determinations for each of the 5 genetical characters applied to 10 pairs formed by different combinations of the 5 endogamous groups. The statistical significance of various differences is shown by asterisks. The group V.N.B. shows a significant difference from C.K.P. for

taste reaction to p.t.c. and color vision, and from D.R.B. and D.Y.B. for color vision only. The other 7 pairs of endogamous groups do not show any significant difference.

TABLE 3

Values of χ^2 for intergroup differences with respect to genetical characters

PAIRS OF ENDOGAMOUS GROUPS	ABO	MN	Rh	p.t.c.	c.v.	GENETICAL DIFFERENCE, X^2
V.N.B. × D.R.B.	0.97	5.31	0.27	1.60	4.03*	1.53
V.N.B. × D.Y.B.	3.91	2.96	3.19	0.67	4.03*	1.85
V.N.B. × K.B	2.10	0.58	3.19	0.52	1.80	1.02
V.N.B. × C.K.P.	2.42	5.81	0.00	5.98**	7.79†	2.75
D.R.B. × D.Y.B.	1.40	0.60	1.68	0.02	0.00	0.49
D.R.B. × K.B.	4.45	2.57	1.68	0.30	0.52	1.19
D.R.B. × C.K.P.	0.89	0.04	0.27	1.42	1.02	0.45
D.Y.B. × K.B.	6.39	0.92	0.00	0.01	0.52	0.98
D.Y.B. × C.K.P.	1.79	0.91	3.19	2.66	1.02	1.20
K.B. × C.K.B.	6.14	3.00	3.19	3.05	2.75	2.26

Statistical significance: * indicates $.05 > p > .02$
** indicates $0.02 > p > .01$
† indicates $0.01 > p > .001$.

Chi-square method. Consider two populations examined for n discrete characters, each character having 2 to r classes. Let p_{ij} be the proportion of j-class of i-character for one population and p'_{ij} for the other.

Let $q_{ij} = \frac{p_{ij} + p'_{ij}}{2}$. The required quantitative measure of genetical difference is given by:

$$X^2 = \frac{100 \sum_{i=1}^{n} \sum_{j=1}^{r} \left\{ \frac{(p'_{ij} - q_{ij})^2}{q_{ij}} + \frac{(p_{ij} - q_{ij})^2}{q_{ij}} \right\}}{\text{Total number of degrees of freedom}}$$

In spite of this clumsy looking formula, X^2 is very simple to compute. Reduce the sample size of each of the two populations to 100 for every character, if it is different; in other words, express the frequency as percentage. Next, calculate the values of χ^2 for the test of homogeneity applied to $2 \times r$ tables for each one of the n characters and pool them. X^2 is obtained by dividing this pooled value of χ^2 by the total number of degrees of freedom.

X^2 is thus essentially χ^2. The reduction to a uniform sample size 100 is introduced to compare the pairs of populations examined for different sample sizes. In order to compare populations examined for different number of characters, all of which are not with the same number of classes, it is adjusted by dividing it by the number of degrees of freedom. It may be noted that X^2 becomes more and more accurate with increase in the number of degrees of freedom and with increase in the sample sizes.

There is no evidence of linkage between any of the 5 genetical characters studied here. This would mean that the characters are independent of one another and would justify the pooling of χ^2 for different characters. It may be worth mentioning that χ^2 should be obtained over $r_i \times r_2 \times r_3 \ldots \times r_n$ cells where r_i are number of classes for the i-character. If the characters are independent, this comes out as a sum.

The last column in table 3 contains the values of genetical difference. The computation is made easy in the present case, as the sample sizes are 100 for every character except p.t.c.

The values of genetical difference for D.R.B. × D.Y.B. and D.R.B. × C.K.P. are 0.49 and 0.45 respectively, the least values in the series. The differences of D.R.B. and D.Y.B. from K.B. are 1.19 and 0.98 respectively and from V.N.B. are 1.53 and 1.85. Thus the differences of these two groups from K.B. and V.N.B. are comparable. The differences of V.N.B. from the other three groups range from 1.02 to 2.75. The difference for K.B. × C.K.P. is 2.26. These differences will be further discussed.

In order to comprehend the extent of the genetical differences between the endogamous groups, the following determination was made: American Whites and American Negroes are two groups for which all the genetical characters studied here have been examined in large samples (quoted in Sanghvi and Khanolkar, '49). The genetical difference between these two groups on the basis of the same 5 genetical characters is 2.95, compared with 2.75 for V.N.B. × C.K.P., and 2.26 for K.B. × C.K.P.

On the basis of the individual values of χ^2 no significant difference was noted between K.B. and C.K.P. for any character. The genetical difference between these two groups is 2.26, which is greater than the difference between two other pairs, viz. V.N.B. $\times$ D.R.B. and V.N.B. $\times$ D.Y.B., which showed a significant difference for one character, namely color vision. It may, however, be mentioned that the individual values of χ^2 also show highly significant differences between K.B. and C.K.P. for OAB and Rh blood groups and taste reactions to p.t.c. with larger sample sizes (Sanghvi and Khanolkar, '49). The genetical difference may thus be of value in indicating the extent of difference with reasonably small sample sizes.

Morphological differences

Kurulkar's data on 11 morphological measurements are analyzed for intergroup differences by the application of t-test to each pair of means compared. Table 4 contains the results of this analysis.

Out of 11 morphological measurements, the groups V.N.B. and C.K.P. differ from each other in as many as 8 characters, whereas the groups D.R.B. and D.Y.B. differ in three, the least number in the series. Consideration only of the number of characters would not throw much light, as it would not take into account the degree of each difference. In order to arrive at a measure of difference, like the one for genetical traits, the following property of t-distribution was utilized. Values of t for a sufficiently large number of degrees of freedom form a normal variate, and then, on the assumption that the morphological measurements are independent of one another, the values of t^2 would be distributed as χ^2 independently of each other. The necessary adjustments for uniform sample size and the number of degrees of freedom applied to the genetical difference can then be applied to the morphological difference also.

t-square method. Consider two populations examined for n morphological measurements. Let m_i be the mean and s_i be

TABLE 4

Values of t for intergroup differences with respect to morphological characters

	GROUP COMBINATION	HL	HB	MFB	BZB	BGB	TFH	UFH	NL	NB	BB	IB	MORPHOLOGICAL DIFFERENCE, τ^2
1.	V.N.B. × D.R.B.	0.07	8.41**	1.88	2.50**	0.61	0.49	2.03*	0.15	7.92**	2.38**	0.19	13.97
2.	V.N.B. × D.Y.B.	1.80	10.66**	1.72	2.81**	2.03*	0.25	3.14**	2.57**	4.84**	3.35**	0.79	16.70
3.	V.N.B. × K.B.	2.63**	6.83**	1.30	1.15	0.86	0.32	1.22	2.37**	6.51**	0.21	2.69**	10.38
4.	V.N.B. × C.K.P.	1.78	7.61**	3.50**	4.85**	2.29*	0.53	3.34**	1.25	2.76**	4.87**	4.16**	14.89
5.	D.R.B. × D.Y.B.	1.68	1.80	0.12	0.49	2.88**	0.87	1.10	3.22**	2.92**	1.10	0.56	3.36
6.	D.R.B. × K.B.	2.66**	1.68	0.59	1.70	0.33	0.96	0.81	2.88**	1.15	2.57**	2.66**	3.47
7.	D.R.B. × C.K.P.	1.58	0.67	1.68	2.89**	1.87	1.21	1.42	1.63	4.23**	2.57**	4.02**	5.86
8.	D.Y.B. × K.B.	4.57**	3.59**	0.46	2.08*	3.06**	0.07	1.91	0.00	1.72	3.52**	3.24**	7.02
9.	D.Y.B. × C.K.P.	0.07	2.47**	1.76	2.25*	4.73**	0.31	0.39	1.47	1.51	1.36	4.62**	5.87
10.	K.B. × C.K.B.	4.40**	0.98	2.27*	4.54**	1.48	0.24	2.18*	1.32	3.08**	5.03**	1.20	8.28

Statistical significance: * indicates $.05 > P > .02$ ** indicates $.01 > P > .001$

** indicates $.02 > P > .01$ *** indicates $P < .001$.

the standard deviation x of i-character for one population and m_i' and s'_i for the other. The required quantitative measure of morphological difference is given by:

$$T^2 = \frac{100 \sum_{i=1}^{n} \left\{ \frac{(m_i - m'_i)^2}{s_i^2 + s'^2_i} \right\}}{n}$$

The assumption that the morphological measurements are independent of each other is not strictly correct, as they are definitely known to be positively correlated. In justification of the procedure adopted here, it may be pointed out that if the correlations between measurements are not unevenly distributed, the effect would probably be to exaggerate to a certain extent the measure of difference. The values in the last column of this table are the morphological differences.

The difference between D.R.B. and D.Y.B. is 3.36, which is the minimum in the series. The differences of these two groups from C.K.P. are 5.86 and 5.87 respectively, and from V.N.B. are 13.97 and 16.70, and are thus comparable. The differences of these same two groups from K.B. are 3.47 and 7.02, not very close, but still comparable. The differences of V.N.B. from the other three groups range from 10.30 to 16.70. The difference between K.B. and C.K.P. is 8.28. These differences will be further discussed.

In order to comprehend the extent of the morphological differences between the endogamous groups, Shapiro's ('51) data of Chinese and Hawaiians for the same 11 measurements were analyzed. The morphological difference between these two groups turns out to be 22.42, compared with 16.70 for V.N.B. × D.Y.B. and 14.89 for V.N.B. × C.K.P.

DISCUSSION

It was mentioned earlier that Risley ('15) and Guha ('31) examined for morphological measurements a large number of individuals belonging to several different groups in India. In Bombay State, both of them studied the same general

groups that were selected for the present investigation; but not precisely the same endogamous groups. They did not study D.R.B. and D.Y.B. separately but studied the group of Desasth Brāhman (D.B.). They did not take notice of the subdivisions in V.N.B., and combined C.K.P. with two other groups which together constitute the grouping Prabhu. Risley studied the differences mainly on the basis of cephalic index. He put all the groups in this region in the same physical type, "Scytho-Dravidian," a type with a range of 77–80 in the cephalic index. Guha arrived at his conclusions by using Karl Pearson's coefficient of racial likeness (C.R.L.). In calculating C.R.L., it is customary not to use the individual variance of each group of people, but to use the variance of one of the large groups studied. Guha selected the group V.N.B. for his estimates of variance. V.N.B., when compared with D.B., K.B., and C.K.P., gave 8.54, 12.24 and 10.97 values of C.R.L., respectively. The values of C.R.L. when the other three groups were compared among themselves were very small, ranging from 0.15 to 0.92. On the basis of these values he discriminated V.N.B. from the other three groups, which he provisionally called the Marathi races. Later on ('37), he designated V.N.B. and the other three groups as "Alpo-Dinarics," the other three groups also containing racial elements of "Orientals."

In the present study, the morphological differences (table 4) between V.N.B. and the other three groups D.B. (i.e. D.R.B. and D.Y.B.), K.B. and C.K.P. vary from 10.38 to 16.70. There is no sudden drop in the values of morphological difference like the one found by Guha in the pairs of the other three groups. The difference between K.B. and C.K.P. is 8.28, that between C.K.P. and D.B. is 5.86–5.87 and that between D.B. and K.B. is 3.47–7.02.

The conclusion regarding a sharp discrimination of V.N.B. from the other three groups, which Guha arrived at by the method of C.R.L. applied to his data, thus is not borne out by the present method of analysis applied to Kurulkar's data. In order to see whether this discrepancy was due to a differ-

ence in the two sets of data or to a difference in the two methods of analysis, the present method of analysis was applied to Guha's data. V.N.B., when compared with the other groups, showed values ranging from 8.22 to 13.16. The values of morphological difference for the other three groups ranged from 1.40 to 4.22. These latter values are higher than the values of C.R.L., but not quite to the extent as found in Kurulkar's data. Part of the discrepancy might, therefore, be accounted for by the fact that Guha was not dealing strictly with the same endogamous groups that were used in the present study.

Comparison of the genetical and morphological methods

In the last section, biological differences between pairs of endogamous groups were arrived at by two different methods (1) based on a study of genetical traits, and (2) based on a study of morphological measurements. In either case the differences were expressed in terms of the contribution to the values of χ^2 by one degree of freedom by a standard sample size of 100 individuals of the pair of endogamous groups under consideration. These two differences are, however, not directly comparable, as the basis of difference in the two cases is not the same. In one case, it is based upon the values of χ^2 obtained by a test of homogeneity applied to the two samples for a discrete character. In the other case, it is based on the t-test applied for comparing the means of a continuous character in the two samples. In order to make the genetical and morphological differences comparable, they were reduced to a comparable scale equivalent to the mean difference between the 10 pairs of endogamous groups. The mean genetical difference is 1.37 units and the mean morphological difference is 8.98 units. Table 5 contains the values of genetical and morphological differences on the new scale. Figure 1 is a graphical representation of these values.

The differences for D.R.B. × D.Y.B. and D.Y.B. × K.B. are almost equal by the two methods. The morphological differ-

ences are larger than the genetical differences for V.N.B. × D.R.B., V.N.B. × D.Y.B., V.N.B. × K.B., and D.Y.B. × C.K.P. and smaller for V.N.B. × C.K.P., D.R.B. × K.B. and D.Y.B. × C.K.P The morphological difference for K.B. × C.K.P. is much smaller than the gentical difference.

TABLE 5

Comparison of the relative values of genetical and morphological differences

ENDOGAMOUS GROUP	V.N.B.	D.R.B.	D.Y.B.	K.B.	C.K.P.
V.N.B.	...	1.11	1.35	0.75	2.00
D.R.B.	1.56	...	0.35	0.87	0.33
D.Y.B.	1.86	0.37	...	0.72	0.87
K.B.	1.16	0.39	0.78	...	1.65
C.K.P.	1.66	0.65	0.65	0.92	...

Values above the diagonal refer to the relative genetical differences. Values below the diagonal refer to the relative morphological differences.

Figure 2 is two dimensional geometrical representation of the relationship among the 5 endogamous groups. This figure is also based on values in table 5. The triangles are drawn first with V.N.B., K.B. and C.K.P. as vertices. The differences between D.R.B. and D.Y.B. are small by both the methods and it has been found convenient to represent these two groups by a circle of corresponding diameter with the center placed to give close approximation to the various relative values. This procedure has allowed for adjustments between these two groups and the other three groups, necessary for two-dimensional representation.

The statistical relationship among the 5 endogamous groups is clearly revealed in figure 2. The relative positions of the groups V.N.B., K.B. and C.K.P. with respect to one another are at corners of a triangle by both the methods and would be comparable by a little shift in the vertex K.B. The position of D.B. (D.R.B., D.Y.B.) is not quite the same in the two cases. The larger morphological difference for V.N.B. × D.B. makes it necessary to put D.B. outside the triangle on

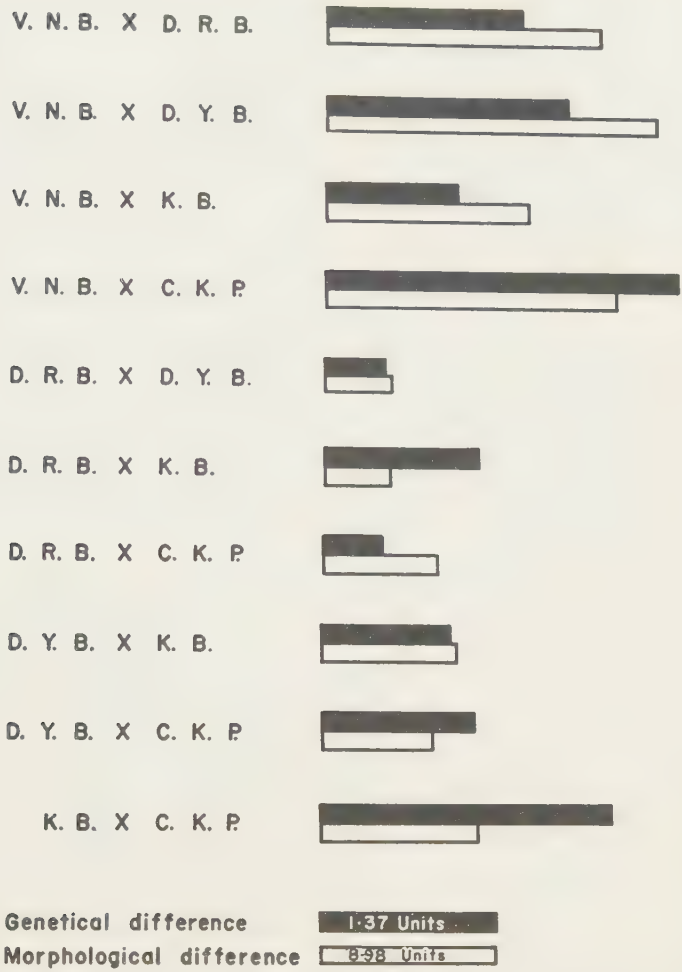
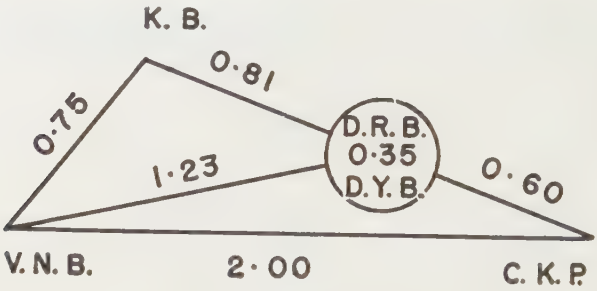


Fig. 1 Comparison of genetical and morphological differences among the 5 endogamous groups.

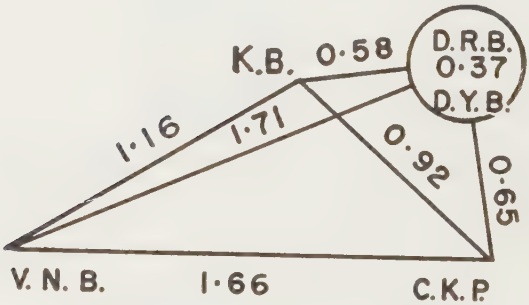
the opposite side of V.N.B., whereas in the genetical case it lies on the triangle on the opposite side to V.N.B.

This study demonstrates an approach for comparing the genetical and morphological methods for evaluating biological differences between groups of populations. Similar studies with larger sample sizes and larger number of characters

will be needed properly to evaluate the two methods. Although one or the other may turn out to be more valuable for elucidating biological relationships in any given case, it is likely that in general the two methods will complement each other. In general it will probably be desirable to use both methods and as many characters for each as is practicable.



GENETICAL DIFFERENCES



MORPHOLOGICAL DIFFERENCES

Fig. 2 Configuration of the 5 endogamous groups based on biological differences arrived at by genetical and morphological methods.

SUMMARY

Two methods are available at present for evaluating the biological differences between groups of populations; one based on a study of genetical traits and the other based on morphological measurements. The present investigation is an attempt to compare these two methods.

The data consist of a study of 5 genetical traits and 11 morphological measurements on 500 unrelated men belonging to 5 endogamous groups in Bombay. The genetical traits studied are ABO, MN and Rh blood groups, taste reactions to p.t.c. and color-blindness. The morphological measurements studied are head length, head breadth, minimum frontal breadth, bizygomatic breadth, bigonial breadth, total facial height, upper facial height, nasal length, nasal breadth, biorbital breadth and interorbital breadth.

Intergroup differences between pairs of endogamous groups are examined by the application of simple statistical tests: χ^2-test for the genetical traits and t-test for the morphological measurements. In order to arrive at a measure of difference based on the entire set of genetical data, an appropriate statistical test is developed. This test depends on the cumulative nature of χ^2 values. A simple property of t-values is used to obtain a measure of difference based on the entire set of morphological data. The results arrived at by these two methods are compared by reducing them to a proper scale.

Studies of more characters on larger samples will be required for deciding which one of the two methods will give results nearer to the existing biological situation. It is very likely that the two methods might reveal a similar relationship, as the present study indicates.

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ENVIRONMENT AND PHYSIQUE.— The effects of climatic conditions are very patent amongst the native peoples of the New World. The Iroquois of the temperate parts (lat. 40°–45°) of North America were a tall, rather light-complexioned race, but as we keep moving south and approach the equator, their kindred tribes grow somewhat darker in complexion and more feeble in physique, except where they live at a considerable altitude, for of course altitude acts in the same way as latitude. When once we pass below the equator the physique keeps steadily improving until we come to the Pampas Indians, a vigorous race who defied all the efforts of the Spaniards to subdue them; and finally we meet the Patagonians (lat. 40°–53°), a fine, tall, light-complexioned race, who form in the south the counterpart of the Iroquois and their closely allied tribes in the north.

The same law, as is well known, can be seen at work in Europe. . . .

If we turn from man to the other animals we find a complete demonstration of this doctrine. . . . — William Ridgeway. The application of zoological laws to man. Report, 78th Meeting of the British Assn. Adv. Sci., Dublin, Sept., 1908, London, 1909, pp. 832–847.

THE SOMATOLOGY OF ULITHI ATOLL

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FOUR FIGURES

The materials which form the basis of this article were collected in 1947 and 1948 by the senior author as a participant in the project known as the Coördinated Investigation of Micronesian Anthropology (CIMA), sponsored by the Pacific Science Board of the National Research Council. Because they constitute a small sample they are merely offered as a modest contribution to the growing body of data on Micronesian physical anthropology, which until recently has been lamentably meager. Speculations as to racial history and affinities have been avoided as being outside the scope of this study, but the interested reader may refer to such works as those of Hunt ('50) and Simmons et al. ('52).

Ulithi Atoll lies 10° north of the equator in the western Caroline Islands. While it is but 85 nautical miles northeast of Yap, it is linguistically and culturally closer to a whole string of islands between it and Truk over 750 nautical miles to the east (Lessa, '50). On January 1, 1949, it had a population of 421 persons, one or two of whom appear to be of recent hybridization. The present sample however is probably "pure."

Fifty-nine males were measured. The mean age is 38, and there are 4 subjects 18 years old or less, these being discarded in such instances where it is felt that measurements or observations would be affected. The youngest subject is 16 and the oldest 69 years of age.

A comparison of measurements from Ulithi with those of other series from this area of the Pacific indicates that the men of this atoll group are substantially within the general Micronesian range. Such differences as do appear show a tendency toward the upper extremes of the real averages. In stature, the Ulithi mean exceeds the over-all Micronesian standard to some extent, but remains within the range of medium height. Absolute head lengths tend to be somewhat greater in Ulithi (with the exception of one series from Pingelap), and thus influence a relatively low cephalic index. Ulithi and Yap share in the characteristic of broader faces and lower facial indices. The only trait, however, in which the Ulithians appear at all divergent from other Micronesians is the absolute breadth of the nose. In this respect they exceed all other groups by from 1 to 4.2 mm. Combined with a relatively small nose height, the greater mean breadth yields a nasal index of 82 compared with the total Micronesian average of 75.5.

It is quite probable that a fair proportion of the differences recorded in face heights, nose heights and their respective indices would be reduced by the observation of larger series, and, especially, the standardization of methods for locating nasion.

An examination of the Micronesian data compiled by Hunt ('50) fails to reveal the existence of any linear gradient for metrical traits in these islands. The paucity of material, together with the numerous exceptional cases, throws doubt upon the significance of any pattern which may at this time be observed. In a relatively homogeneous area such as this the use of anthropometry to discriminate local somatological differences is a questionable procedure, though its value may in the future be considerably enhanced by combination with serological and other data for the purpose of genetic linkage analysis.

Table 1 records the means and standard deviations for the various gross measurements and indices of Ulithi males.

Table 2, adapted from Hunt ('50), shows the means for a west to east sequence of Micronesian Islands and includes the

TABLE 1

Measurements and indices: Ulithi males

MEASUREMENTS [1]	N	MEAN	S.D.
Head length	56	19.5	.736
Head breadth	56	14.5	.477
Head height	55	13.2	.418
Cephalic index	56	74.6	3.286
Length-height index	55	67.9	2.679
Breadth-height index	55	91.1	3.576
Cranial module	55	15.8	.405
Minimum frontal	56	10.7	.362
Fronto-parietal index	56	73.6	2.493
Bizygomatic	56	14.3	.630
Cephalo-facial index	56	98.1	3.140
Zygomatic-frontal index	56	75.1	2.916
Bigonial	55	10.6	.540
Zygomatic-gonial index	55	74.5	3.476
Total face height	55	12.2	.720
Total face index	55	85.9	4.951
Upper face height	52	7.2	.442
Upper face index	52	50.4	2.859
Forehead height	41	7.0	.... [2]
Nose height	56	5.5	.376
Nose breadth	56	4.5	.292
Nasal index	56	82.0	5.987
Nose length	56	5.1	.354
Nose salient	56	2.0	.216
Bi-ocular breadth	55	9.4	.457
Inter-ocular breadth	55	3.6	.357
Stature	56	163.5	4.232
Sitting height	56	88.3	2.701
Rel. sitting height	56	54.0	1.173
Trunk height	56	56.7	1.884
Rel. trunk height	56	34.7	1.083
Chest breadth	56	26.9	1.489
Chest depth	56	21.8	2.389
Thoracic index	56	81.2	4.385
Biacromion	55	37.3	1.407
Rel. shoulder breadth	55	22.8	.849
Bi-iliac	56	28.4	1.699
Rel. hip breadth	56	17.3	.902
Shoulder-hip index	55	76.2	4.082
Upper arm length	56	31.6	1.497
Lower arm length	56	24.8	1.193
Brachial index	56	78.5	3.095
Lower leg length	55	37.1	3.254
Weight	56	144.4	17.558

[1] All measurements are recorded in centimeters, except for weight, which is in pounds.

[2] Not calculated since N is below 50.

TABLE 2

Means of measurements and indices: Micronesian males[1]

AREA: OBSERVER: NO. IN SERIES:	TOBI HASEBE 6	SONSOROL HASEBE 11	PALAU HASEBE 134	YAP HUNT 347	ULITHI LESSA 55	W. CAR. IS. HASEBE 41	TRUK HASEBE 164	PONAPE HASEBE 150
Stature	156.80	164.40	160.90	160.30	163.50	163.80	161.60	162.10
Chest girth	84.00	88.62	86.08	....	90.51	88.66	84.03	85.30
Head length	19.11	19.45	18.52	18.85	19.50	19.43	18.97	19.28
Head breadth	13.91	13.85	14.97	15.01	14.53	14.31	13.91	14.21
Cephalic index	72.80	71.30	80.90	79.60	74.60	73.70	73.40	73.70
Face height	12.16	13.08	12.37	11.72	12.21	12.51	12.36	12.67
Face breadth	13.63	13.83	14.12	14.50	14.25	14.06	13.66	13.92
Facial index	85.60	94.50	87.60	81.00	85.90	89.10	90.60	93.30
Nose height	5.20	5.95	5.50	5.48	5.49	5.55	5.57	5.95
Nose breadth	4.40	4.32	4.16	4.17	4.49	4.23	4.31	4.24
Nasal index	84.70	73.10	76.20	6.20	82.10	76.50	77.70	71.60

[1] Adapted from a table compiled by Hunt ('50). All measurements are recorded in centimeters.

Ulithi series for comparative purposes. This represents only a portion of the table used by Hunt, but is felt to be adequate for indicating relationships.

Turning to non-metrical observations, we find that Ulithians are predomiantly light brown in skin color, although exposure to the sun produces a medium brown color. The hair is black, with some instances of red brown, dark brown, and various combinations of these. Greyness is infrequent. While children were not included in the sample it should be pointed out that blondness is sometimes present among them. Head hair is predominantly wavy and coarse, with little incidence of baldness; body hair is sparse. The iris of the eye is usually medium or dark brown with a homogeneous distribution of the pigment. Over half the subjects have no eye fold, but when it is present it is usually lateral or epicanthic.

The profile of the nasal bridge, excluding the tip of the nose, shows considerable variation in shape, with no special dominance of one type or another. The bridge and root of the nose are usually low. The axis of the nostrils is transverse. The lips are usually thick and the lip seam medium or marked.

Ulithians have a slight overbite. Median and lateral shovel-shaped incisors are simultaneously present about 45% of the time. It is interesting to note that while this frequency is extremely low as compared with Chinese, Japanese, and Indians, it is somewhat higher than for Whites and is close to the frequency for American Negroes. Compared with Hawaiians the occurrence is much less frequent (cf. Dahlberg, '45). Dental caries is remarkably low and is more apt to be apical than gingival. Even allowing for the fact that the search for caries was a relatively cursory one, substantiation of the excellence of Ulithian dentition is seen in the fact that relatively few teeth are missing and more than half of the subjects are in possession of all their teeth. The greatest incidence of caries is in the youngest age bracket, possibly reflecting the effects of the war or changed diet. Tooth loss appears to be

due more to pyorrhea resulting from heavy tartar deposits than to caries, there being an excess of calcium in the food.

In the belief that considerable value adheres to the examination of photographs for gaining an over-all impression of physical type, the reader is referred to the pictures presented in figures 1–4. Obviously, the assurance of homogeneity given by the anthropometric data is misleading. The non-metric data, when analyzed, indicate a diversity confirmed by these photographs, which are fair representations of the kinds of men who live on the atoll. One may feel inclined to recognize features which have variously been labelled "Oceanic Negroid," "Negritoid," "Mongoloid," "Indonesian," "Generalized Micronesian," and the like, by various investigators, but no attempt has here been made to segregate either these or other types, both because the sample is too small and because it would be wise to use serological and other data genetically studied.

The authors are grateful for the aid given by the Pacific Science Board and the University of Chicago in making this field study possible, and for a subvention from the Research Committee of the Academic Senate of the University of California at Los Angeles in preparing the materials for publication.

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1 and 2 Representative physical types of Ulithi Atoll.

3 and 4 Representative physical types of Ulithi Atoll.

METHODS OF STUDYING THE BIOMECHANICAL SIGNIFICANCE OF BONE FORM [1]

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FIFTEEN FIGURES

Anthropologists, anatomists and surgeons have been interested in the biomechanical significance of bone form for many years. Most of the early workers on the subject were primarily concerned with an interpretation of the functional significance of the orientation of the trabeculae, but it is only within relatively recent time that stresses and strains have been studied in intact bones. The various methods used in studying the problem may be classified into three groups. The first method consists of mathematical analysis of the stress and mechanical behavior of sections of bones. The second method is based upon a study of stresses and strains produced in models of bones. The third method involves a study of the stresses and strains produced in intact bones. In the second and third methods, recently developed engineering techniques for analysis of strain and stress in engineering structures and materials have been employed.

Since a study of the biomechanical significance of bone form involves the use of engineering techniques, it is well to have a clear understanding of the terminology generally employed in engineering. One of these terms is *force* which is simply defined as a push or a pull. Another term is *energy*, the capacity to do work. Force is the more commonly used term, although in most instances energy is the preferable one as its magnitude is more easily determined. Forces may be

[1] This investigation was supported (in part) by Research Grant RG-1925(C3) from the National Institutes of Health, United States Public Health Service.

classified into three main kinds. *Tensile* (tension) forces which tend to pull an object apart; *compressive* (compression) forces which tend to push an object together; and *shearing* (shear) forces which tend to make one part of an object slide or glide with respect to another part of the same object.

Other terms which are often incorrectly used as synonyms are *strain* and *stress*. Strain is the change in linear dimensions which occurs in an object to which an outside force has been applied. Stress is the intermolecular resistance within the object to the deforming action of the outside force. An example of strain is the tendency for the leg bones to be shortened under the weight of the body when standing erect. Stress is the resistance within the bones to the tendency to be shortened by the body weight. Strain, if sufficiently great, can be seen but stress must be computed.

Stress and strain can be quite easily demonstrated (fig. 1) by the behavior of a column under different types of loading. Figure 1 a is an example of a column which is concentrically loaded. In this condition the entire cross section of the column is subject to compressive (c) stress throughout. However, if the column is eccentrically loaded (fig. 1 b) the column will be bent. This bending produces tensile (pulling apart) stresses and strains (t) on the convex side of the bent column and compressive (pushing together) stresses and strains on the concave side of the column. The magnitude of these stresses and strains is greatest at the surface of the column and gradually diminishes as we pass inward, until finally a plane is reached (the neutral plane or axis) at which the magnitude of the tensile and compressive stresses is zero. This is essentially the behavior of the femur when standing erect. When a force perpendicular to the long axis of a column is applied to the middle of that column, it also produces bending which gives rise to tensile stresses and strains on the convex side of the column and increased compressive stresses and strains on the concave side of the column at the point of the application of force (fig. 1 c). When a force is applied to the side of the femur or any other long bone it behaves in this man-

ner. Finally, when a torsion or twisting force is applied to the opposite ends of a column (fig. 1 d) the ends will be twisted in opposite directions with respect to one another.

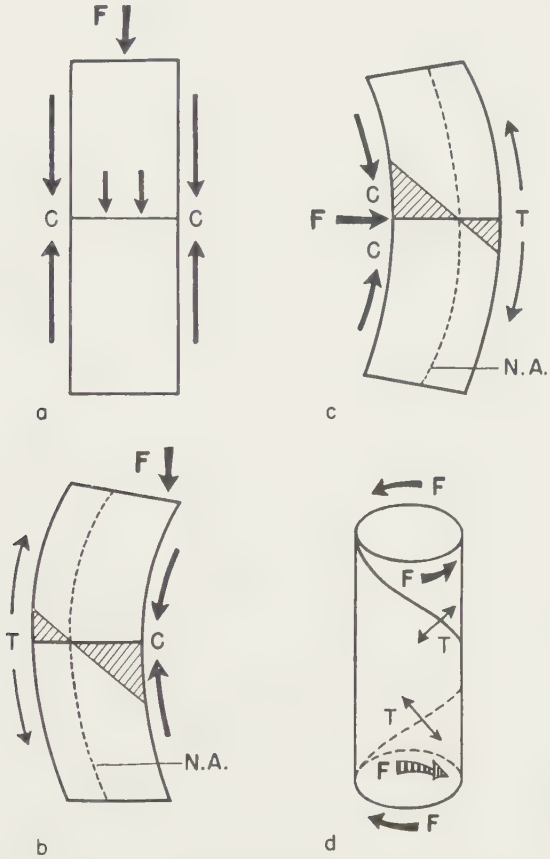

Fig. 1 The behavior of a column under different types of loading (after Evans, '52). See text for explanation.

a. A column under concentric vertical loading.
b. A column under eccentric vertical loading.
c. A column under transverse loading.
d. A column under torsion loading.
C = compression. F = force. N.A. = neutral axis. T = tension.

The large arrows indicate the direction and point of application of the force. The small arrows indicate the direction of the strain.

The tensile stresses and strains which result from the twisting take a spiral course around the column at approximately a 45° angle to its long axis. Such a spiral pattern of tensile strain also occurs in long bones which are similarly twisted. The behavior of the femur under these various types of loading, as well as the areas of tensile and compressive strain, have recently been described by Evans ('52). Let us now discuss some of the major work done by means of each of the three chief methods previously mentioned.

MATHEMATICAL ANALYSIS OF SECTIONS OF BONES

This is the method which was originally employed and has been most extensively used in trying to analyze the functional significance of the organization of spongy bone.

von Meyer in 1867 published a monograph showing trabecular orientation in sections of various bones of the human body. von Meyer reproduced Culmann's famous diagram of a Fairbairn crane, in which he had computed the lines of maximum internal stress (or trajectories). In these computations Culmann assumed that the crane was a homogeneous solid structure approximating the femur in shape and loading. It was considered that a load of 30 kg was applied to the crane in the region corresponding to the acetabulum. As a result of this study Culmann concluded that the trabeculae, as seen in a frontal section of the proximal end of a femur, were laid down along the lines of maximum internal stress in the bone. Thus, the femur could transmit a maximum load with a minimum of material. This diagram or analysis is the basis for the "Trajectorial Theory" of bone form. This theory holds that in spongy bone the trabeculae follow lines similar to the trajectorial lines in a mechanical structure which resembles a bone in form and loading. In other words, the trabeculae are actual trajectories or lines of maximum internal stress within the bone.

In spite of the fact that a bone is not a solid homogeneous structure and that a Fairbairn crane does not actually resemble a femur too closely in shape, the trajectorial idea of

the functional significance of the orientation of the trabeculae within a bone has had wide acceptance. It has also given rise to considerable literature, most of which is concerned with the trabeculae in terms of the stresses and strains to which the bone was presumed to be subjected in the living body. Thus, von Meyer (1867), Wolff (1870), and Roux (1885) all accept the "Trajectorial Theory" and believe that the trabeculae are arranged in accordance with exact mathematical laws. This work culminated in 1892 with the publication of Wolff's famous "Law of Bone Transformation," according to which every change in the form and function of a bone results in changes in orientation of the trabeculae and the external form of the bone. All these changes are assumed to be in accordance with mathematical laws.

von Meyer, Roux, and Wolff all believed that tension was the type of force primarily responsible for bone growth. This, however, has been vigorously denied by Janssen ('20) and Carey ('29). Janssen examined sections of many normal and pathological bones, pointing out many instances where the region of the bones presumably subjected to tensile stress had actually atrophied. Conversely, the regions of the bone subjected to compressive stress had hypertrophied. In contrast to von Meyer, Wolff, and Roux, who did not consider muscle action at all, Janssen believed that the jerking pressure of muscles combined with gravity was the chief mechanical stimulus for bone form, at least in the vertebral column.

Carey also emphasized the role of muscles in determining the orientation of the trabeculae. He studied many sections, in different planes, of the major joints of the body and concluded that the architecture of the spongiosa was entirely determined by the "back pressure vectors" of the muscles acting on the joints. However, he did not attempt to determine the magnitude of the presumed muscle vectors, nor did he consider that in movements of joints the direction and magnitude of the vectors would be constantly changing.

One of the severest critics of the "Trajectorial Theory," according to Murray ('36), was Triepel, who completely de-

nied the theory. Triepel pointed out that trajectories are lines drawn a prescribed distance apart from a number of more or less arbitrarily selected points, and are, therefore, infinite in number. Consequently, if all possible trajectories were drawn they would arise from every point on the margin of the trajectorial diagram, which would be completely blacked out. Thus, if the "Trajectorial Theory" were true there should be no spongy bone as it would all be compact. Triepel also emphasized that in engineering, when trajectorial diagrams are drawn, it is assumed that the body being studied is a solid homogeneous structure, a situation not true for bones. Another criticism was that in many instances the presumed tensile and compressive resisting trabeculae do not cross one another exactly at a right angle as they should according to the "Trajectorial Theory."

One of the most extensive attempts ever made at mathematical analysis of the functional significance of bone form was Koch's paper "The Laws of Bone Architecture," which was published in 1917. In this paper Koch studied 75 cross sections from the femur of an accidentally killed 200 pound Negro man approximately 35 years of age. Each cross section was analyzed mathematically with respect to its center of gravity, neutral axis and neutral surface, moment of inertia, bending and torsional strength, and tensile, compressive and shearing stress, in the same way that an engineer would analyze sections of an engineering structure. He then computed the magnitude of the maximum tensile and compressive stress of the various sections under an assumed load of 100 pounds vertically applied to the head of the femur (fig. 2). In addition, he computed the intensity of the maximum tensile and compressive stresses in the head of the femur under the same assumed conditions. The maximum unit compression and tensile stresses under a load of 160 pounds due to walking and a load of 320 pounds due to running were also calculated.

More recently Marique ('45) has restudied the resistance of the femur by means of mathematical analyses of sections

of the bone. He also determined the moment of inertia, the neutral axis, flexion with and without torsion, and other mechanical properties of the bone. However, he supplemented this work by actual measurements of the strains in the femur by means of Huggenberger extensometers.

Other workers, at one time or another, have also attempted mathematical analysis of the mechanical behavior of bones. However, the papers of Koch and Marique are two of the most extensive studies in which this method had been used.

In spite of its ingenuity, mathematical analysis of the biomechanical behavior of the bones can be criticized on several counts. The first is that in such studies it is assumed that the bone is composed of uniform homogeneous material throughout. Such, however, is far from the conditions as they occur in an actual bone. Secondly, the results of mathematical studies are in two dimensions instead of three as is the case with an actual bone. Thirdly, the formulae which are used in the various mathematical determinations of the physical properties and mechanical behavior of the bone are those derived from similar studies on metals (steel) and actually may not be applicable to the conditions as existing in bone.

STUDIES OF STRESS AND STRAIN IN BONES BY MEANS OF MODELS

One of the first attempts to study stresses and strains in bone by means of models was that of Roux (1885) who made a rubber model of an ankylosed knee joint and coated it with melted paraffin. The model was then loaded in a way similar to that which Roux assumed had occurred in the knee of the living individual and the cracks produced in the melted paraffin were studied. From these cracks Roux drew several trajectorial diagrams of the knee joint. As he accepted the "Trajectorial Theory" of the functional significance of the orientation of the trabeculae in spongy bone, it was assumed that certain of the trabeculae or trajectory lines were compression resisting and others were tension resisting. How-

ever, the magnitude of the pressure and tension was not indicated and Roux's analysis has been strongly criticized by Janssen (op. cit.) on the grounds that the trajectorial diagrams did not correspond with photographs of the actual specimen. Furthermore, the trajectories, as drawn by Roux, did not behave the way they should have according to the "Trajectorial Theory."

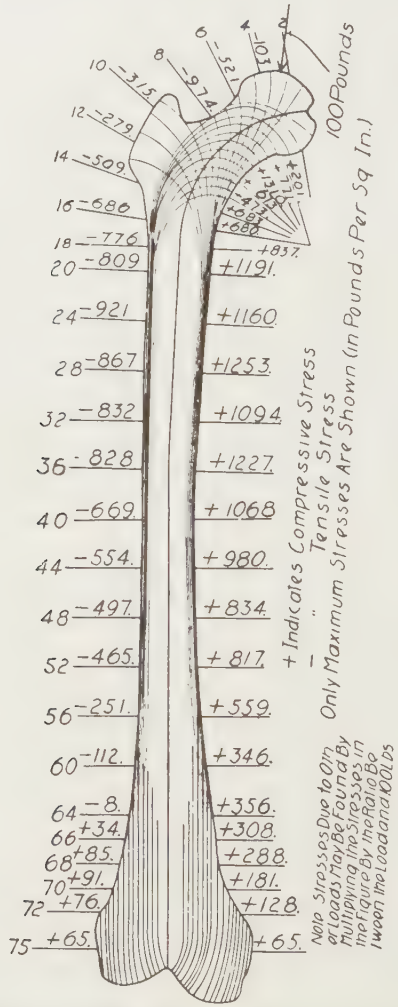

Fig. 2 The tensile and compressive stresses in the femur under an assumed load of 100 pounds (after Koch, '17).

More recently stresses and strains in bone have been studied by means of photo-elasticity. In this procedure a plastic model of the bone is made and then loaded in various ways. The stress patterns produced in the plastic model are then studied under polarized light. The underlying principle of such studies is based on the fact that polarized phenyl formaldehyde resins become birefringent under stress. At this time they behave somewhat like temporary crystals whose molecular structure is reoriented along the lines of stress. These lines are then evident when the model is examined under polarized light. When a white light is used all the colors of the spectrum are displayed in the stress patterns. However, when photographed the stress pattern appears as alternating bands of light and shadow. The stress pattern is not changed, either quantitatively or qualitatively, by using monochromatic light, as is done in engineering practice. The change from solid light color to a dark band, back to a white band and then to a dark band occurs under known conditions of loading. For example, if the plastic specimen were all white unloaded and then a dark band appeared when 25 pounds was applied, then an additional load up to 50 pounds produced a white band and continual loading up to 75 pounds produced another dark band, it would be known that each dark band represented an increased load of 25 pounds. Thus, it is possible to determine accurately the load necessary to produce a given stress pattern by means of photo-elastic studies.

This technique is quite extensively used by engineers for stress-strain analysis of mechanical structures. With appropriate methods the stresses in the model can be calibrated and an accurate mathematical analysis made of the actual internal stresses in the original object. By heating the model the stress pattern can be "frozen" and then sections made after the model has been cooled so that the internal stress can be studied. Thus, a three dimensional concept can be obtained of the object being tested.

Photo-elastic methods have been used by Milch ('40), who studied stress patterns produced in models of the normal femur, models of femurs representing various orthopaedic procedures, and a model of the calcaneum. For this purpose, models were cut from flat plates of catalin three-eighths of an inch thick. These models were then loaded in various ways and the resulting stress patterns studied under polarized light (fig. 3). Photo-elasticity has also recently been used by Pauwels ('51) in studying the femur and humerus.

The objections to a study of bone form by photo-elastic methods are, as previously pointed out by Milch (op. cit.), (1) bone is not a homogeneous crystalline material, (2) the physical properties of a given bone vary from one time to another within the same individual, and (3) the shape of bone is also the result of a variety of different types of forces acting in different combinations under various conditions. Additional objections are that the method used by Milch is only a two dimension concept instead of a three dimensional one such as exists in an actual bone. Another objection is that the plastic model is a solid structure whereas a bone is not, especially a long bone the kind which has been most extensively studied by means of this method.

STRESS AND STRAIN IN INTACT BONES

One of the first investigators to apply, to a study of whole bones, methods used by engineers for stress-strain analysis in intact engineering structures was Küntscher ('34, '35a, '35b). He used a method, developed by Dietrich and Lehr of the Maybach works, which was employed in testing machine parts for points of weakness and failure. The method is based upon Hook's Law that stress is directly proportional to strain. It consists of coating the object to be tested with melted colophonium. The colophonium was heated until it actively foamed and then cooled until gas bubbles no longer appeared. If the colophonium were applied while it was boiling it would blister and then could not be used. The object coated with the colophonium was then loaded in various

ways and cracks appeared in the colophonium as a result of the tensile strain in the object which had been coated. These cracks arose at the areas of highest tensile strain where failure in the part would occur if a sufficient load were applied.

Küntscher applied this technique to a study of stress and strain in the various long bones of the body. He found that a coat of colophonium 1 mm thick was best, as the cracks were easily visible and showed in a photograph (figs. 4 and 5) without special marking.

With this method Küntscher studied the tensile strain patterns produced in normal and pathological bones under various types of loading. However, the magnitude of the load producing the tensile strain patterns indicated in the photographs of his various specimens was not given, although he stated that a load of 26 kg on the head of the femur of a 154 pound man produced cracks in the colophonium on the neck of the bone. Also, the age of the individuals whose bones were studied is not given. When a bone was studied under tension it was removed from the melted colophonium after the air bubbles had gone and then cooled. If it were to be studied under compression, the bone was first loaded in a testing machine and then coated with the colophonium which was allowed to cool. In the tension studies cracks appeared in the colophonium as the load was gradually increased; in the compression studies they appeared as the load was gradually decreased.

A somewhat similar method for analysis of stress and strain in engineering materials was developed in 1940 by deForest and Ellis. In this technique a brittle lacquer, given the trade name "Stresscoat," is sprayed upon the object to be tested. Here, also, the lacquer cracks in response to tensile deformation in the underlying material, the site where the cracks first appeared being the area of highest tensile strain where failure would occur. The "Stresscoat" technique is considerably easier to use than is Küntscher's colophonium method, as the lacquer is applied to the test object with a spray gun. Consequently, it is well impregnated with air bubbles, the

effect of which is that the cracks in the "Stresscoat" lacquer are continuously being interrupted by these bubbles and therefore continue to be propagated in the direction of the tensile strain in the underlying material. Although the cracks of colophonium also arose from tensile deformation in the underlying material, their further propagation was without regard to the stress conditions in the material. A very high tensile stress concentration existed at the end of the cracks in the colophonium and the continued propagation of the cracks would be in their initial direction because the colophonium was homogeneous and of a uniform thickness. An additional advantage to using "Stresscoat" is that it does not need to be heated, whereas Küntscher found that colophonium had to be heated to slightly less than 40°C. to get the proper results. Furthermore, the sensitivity of the "Stresscoat" lacquer can be quite accurately determined in inches/inch, but the sensitivity of the colophonium, although not stated by Küntscher, would undoubtedly be considerably less than that of "Stresscoat" as it had to be applied in a much thicker layer.

The first investigators to adopt the "Stresscoat" technique to a study of stress and strain in intact bones were Gurdjian and Lissner ('45), who have used it in an extensive series of studies on skull deformations and fracture in man and some of the lower mammals. One of the first questions investigated was whether or not the "Stresscoat" strain pattern produced in a dry bone was similar to that which would be produced under corresponding test conditions in the bones of a living animal. In order to investigate this problem Gurdjian and Lissner ('45) made a series of studies on the skull of 6 dogs and a monkey. In the first study the scalp of the anesthetized animal was reflected, the exposed bones coated with "Stresscoat" and a blow applied to the skull. The "Stresscoat" pattern obtained under these conditions was then traced with India ink and photographed. In a second series of studies the procedure was repeated in the dead animal with the skull contents intact. Here also, the resulting "Stresscoat" pattern

was photographed. Finally, the skull was removed from the animal and dried and the test repeated on the dried skull of the same animal and the resulting "Stresscoat" pattern photographed. Examination of the "Stresscoat" pattern obtained in the monkey (figs. 6–8) under the above described conditions showed that the pattern produced was essentially similar regardless of the experimental conditions at the time of the test. These tests showed that the "Stresscoat" patterns in a dry bone are essentially similar to those which would be obtained in living bone with the exception that the extent of the pattern in living bone is slightly greater. In a later paper ('47), Gurdjian, Lissner and Webster studied the "Stresscoat" or strain pattern produced on the inner and the outer aspect of the skull under known experimental conditions (figs. 9 and 10). By use of this technique, Gurdjian and Lissner have conclusively shown that linear skull fractures arise from failure of the bone because of the tensile stresses in it.

The "Stresscoat" technique has also been used by Evans, Lissner, and Pedersen in studying deformations and fractures produced in the femur under various types of loading in different orientations of the bone ('48a, '48b, '49). These investigators also found, as in the case for the skull, that linear fractures of the femur arose from failure of the bone as a result of the tensile stress within the bone. Figures 11 and 12 illustrate a "Stresscoat" deformation pattern produced in a femur and a mandible.

The tensile strain patterns produced by means of the colophonium and the "Stresscoat" techniques give an overall view of the areas of tensile strain produced in the bone by various types and points of loading. However, if one wishes to measure very accurately the actual extent or magnitude of the strain other techniques must be used. Thus, Küntscher ('36) and Marique (op. cit.) used Huggenberger extensometers (fig. 13) in order to measure the actual magnitude of the strain or deformation produced in the bone during various tests.

Another method of measuring very minute strains or deformations in a material is by the use of electric strain gages of the SR4 type. These have been used by Gurdjian and Lissner ('44) in studying the mechanism of head injury. The strain gage was connected with a cathode ray oscilloscope so that a permanent record could be obtained of the strain or deformation by photographing the oscilloscopic screen.

Evans, Coolbaugh, and Lebow (unpublished) have also used SR4 strain gages to study the strains occurring in the tibia of a living dog while walking around. The strain gage was attached to an exposed area on the tibia of the dog and the deformations occurring in the bone were recorded on an oscilloscope to which the strain gage was connected (figs. 14 and 15).

By use of the "Stresscoat" technique one could determine in advance the overall strain pattern and where to place strain gages in order to have a very accurate measurement of the magnitude of the strain in a local area.

CONCLUSIONS

From the foregoing discussion it is seen that many of the techniques employed by engineers for stress-strain analysis in engineering structures and materials are also applicable for studying similar phenomenon in bones. By these means one may study the stresses and strains produced in bones under controlled conditions of loading and orientation in which the magnitude of the load or the energy applied to the bone, as well as its point of application and direction, can be controlled. It is thus possible to obtain some idea of the behavior of the bone as a mechanical structure or unit. It is, of course, obvious that the experimental conditions employed in such studies are far more simple than those occurring in the bones of a living animal. In the latter case, stresses and strains to which the bone is subjected are constantly changing during different phases of locomotion or movement. It has also recently been shown by Coolbaugh ('52) that a reduction in the blood supply to a bone has marked effects on

its physical properties and hence its mechanical behavior. Regional differences in the physical properties of the human femur have been studied by Evans and Lebow ('51) who found that the areas subjected to tensile strain, as revealed by "Stresscoat" studies of the femur under static and dynamic vertical loading, also have the highest average tensile strength. More recently the same authors ('52) have shown considerable differences in the physical properties of the various bones of the inferior extremities in a single individual. All these factors, as well as age, sex, state of health, and nutrition influence the biomechanical behavior of bones.

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PLATES

PLATE 1

EXPLANATION OF FIGURES

3 Stress pattern, as seen by polarized light, in a plastic model of a femur under compression (after Milch, '40).

Tensile strain patterns (figs. 4–5) produced in colophonium coated bones (after Küntscher, '34). See text for explanation.

4 Femur under compression loading.

5 Tibia under torsion loading.

"Stresscoat" deformation patterns (figs. 6–8) produced in the skull of a macaque monkey by a fronto-parietal blow at the midline (after Gurdjian and Lissner, '45). See text for explanation.

6 Pattern in the skull of a monkey under nembutal anesthesia.

7 Pattern in the skull of the dead monkey with skull contents intact.

8 Pattern in the dry skull of the same monkey.

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PLATE 2

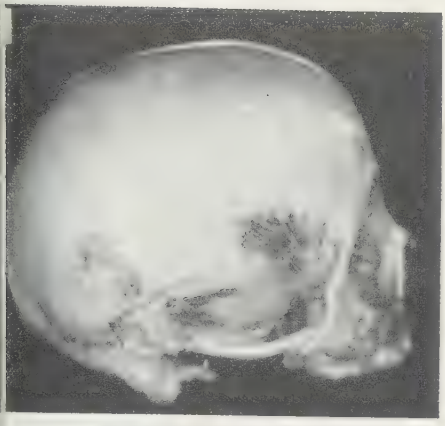
EXPLANATION OF FIGURES

9 ''Stresscoat'' deformation pattern produced on the outer aspect of an adult human skull by a right lateral parietal blow (after Gurdjian, Lissner, and Webster, '47). The point of impact is surrounded by a region devoid of ''Stresscoat'' cracks. This region corresponds to the stellate pattern (fig. 10) on the inner surface of the skull. The cracks on the external surface arise from outbending in at least three directions: (1) in a superoinferior direction, anteriorly, (2) in a superior inferior direction, below, and (3) in an anterior posterior direction, posteriorly.

10 ''Stresscoat'' deformation pattern on the inner aspect of the same skull. Note that the stellate pattern is opposite the point of impact on the outer surface of the skull (fig. 9). The pattern is cut short superiorly by the curving of the skull.

11 Tensile strain pattern produced in a ''Stresscoated'' left femur by 11.8 inch pounds of energy applied to the one-fourth point of the posterior aspect of the shaft. The tensile strain producing the pattern was 0.0006 inches/inch.

12 Deformation pattern produced in a ''Stresscoated'' human mandible by a load of 175 pounds (maximum) applied to a three-fourths inch brass rod laid across the body of the mandible near its angle. The pattern was produced by a strain of 0.00065 inches/inch.



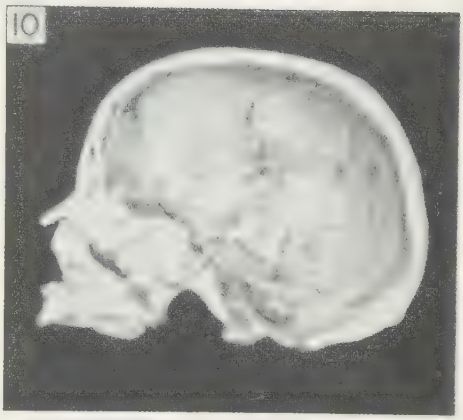

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PLATE 3

EXPLANATION OF FIGURES

13 Use of Huggenberger extensometers for measuring the magnitude of the strain produced in the neck and the shaft of a femur by vertical loading of the head of the bone (after Marique, '45).

14 An SR4 electric strain gage on the tibia of a living dog.

15 Oscilloscopic record of the strains, as recorded by an SR4 gage (fig. 14), occurring in the tibia of a walking dog. The spikes above the base line indicate tensile strain and those below the line represent compressive strain.

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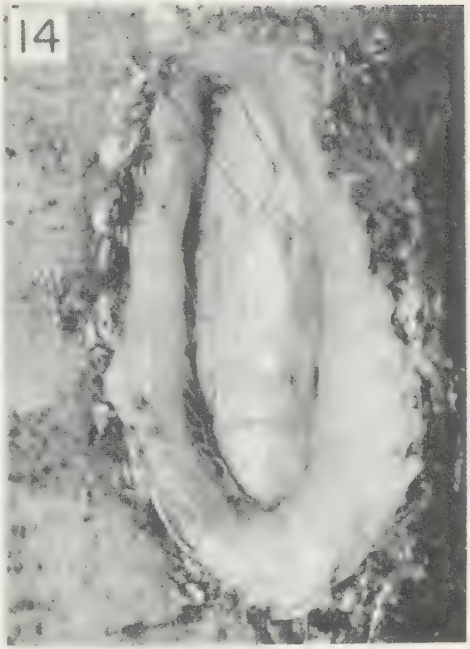
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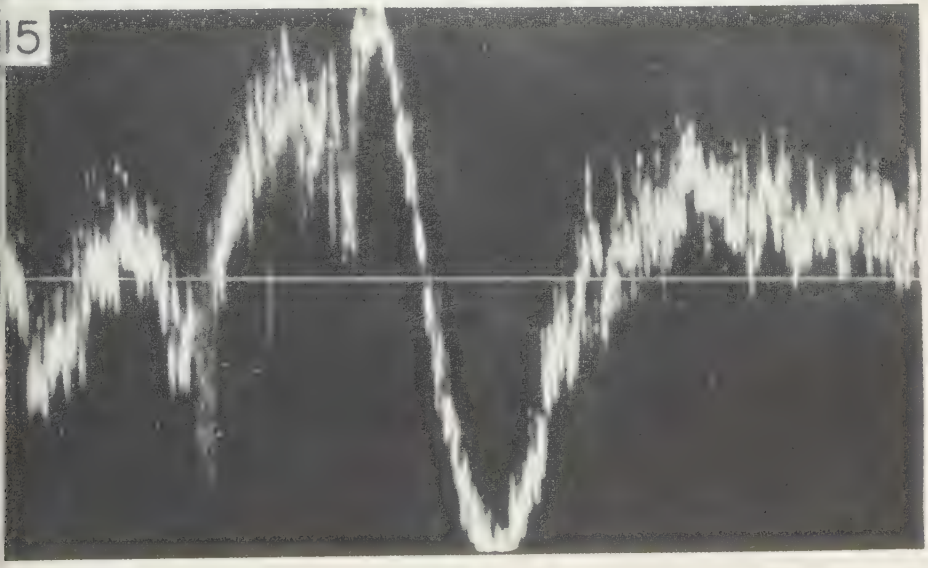
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Physique of Returned Japanese Emigrants.—". . . The height and weight of Nisei children of primary schools are significantly greater than those of other children and greater than the national [i.e. Japanese] average. This evidences the fact that life in Canada is far better for the growth of infants than life in the home village. . . . The physique of Niseis . . . is drawing the attention [i.e.in the Japanese village] of many people. The same survey on children shows also that Nisei children have more bad teeth than other children, perhaps because the former eat confectionaries more than the latter, but the cases of trachoma are much fewer among Nisei children than among other children [in the Japanese village] as a result of a relatively stronger sense of sanitation of the ex-emigrants." (P. 32.) Influences of emigrants on their home village. Report of a Survey of "Amerika-Mura." For Population Problems Research Council, Mainichi Newspaper Publ. Co., Tokyo, 1953, 36 pp. (The emigrants concerned derived from the fishing village of Mio-Mura in southwest Honshu, and settled a small fishing community near Vancouver; recent return migration has swelled the original village from 1,200 [1926] to 1,700 in 1951.)

BRIEF COMMUNICATION

A NEW INTERNAL CASTING METHOD

DONALD J. TUGBY
National Museum of Victoria, Melbourne

TWO FIGURES

Comparative studies of the gross morphology of the homonid brain have been limited in their effectiveness by the lack of suitable fresh material. In the study of non-living types, the use of casts was always necessary where they were obtainable. Often, however, workers from Gall to the latter-day students of brachycephalization have used the form of the skull as an index of psychological development or "advancement." Where recourse was had to casts of the cranial cavity, the limiting factor in deciding the extent of the study was the validity and effectiveness of the casting method used. Furthermore, for rarer specimens, it was not always possible to obtain even a cast owing to the risk of possible damage to the specimen. The development of a new method which obviates damage to the specimen and which provides greater detail is therefore of some interest.

The technique used in this method has been more fully described elsewhere (Tugby and Boswell, '53); this brief communication outlines its raison d'etre, briefly describes the technique itself, and discusses its further development and limitations. The handling of the casting medium was developed by Mr. P. C. R. Boswell, Preparator to the National Museum of Victoria. Briefly, the method consists of the application of successive layers of rubber latex to the inside of a cranium whose openings have been blocked by clay or sticking plaster. Each layer is cured in turn by directing a current of hot air through the foramen magnum. After loosening with hot water, the latex cast is withdrawn through

the foramen magnum and immediately resumes the shape of the inside of the cranial cavity. Attention has to be paid to the proper cleaning of the specimen, the binding of the latex layers and curing time.

The validity of the method has been determined by comparison of the tracings from radiographs of the outline of the cast and corresponding skull oriented in the same plane by means of a Broadbent Encephalometer. A slight all-round shrinkage is noticeable in the casts, amounting to about 4 mm in the worst case. This shrinkage is a function of the curing process, both time and temperature being important factors. The general form of the original is well preserved in all cases.

In comparison with plaster casts, the most striking feature of casts made by this method is the amount of detail obtained. This is especially evident in respect of the blood supply as represented by grooves on the inner surface of the cranium (fig. 1), the foramina and canals in the base of the cranial cavity and the sutures.

The presence of all these features enables not only their ontogeny and phylogeny to be investigated, but makes easier the location of different parts of the brain with reference to the landmarks of the skull. Comparative accounts of developmental patterns are thereby facilitated.

Casts may be obtained from non-human skulls with relatively small foramina magna. An almost perfectly valid cast was obtained from a young male *Pongo pygmaeus* (Nat. Mus. No. R 7709), whose diamond-shaped foramen magnum measured 2.8 cm long by 2.5 cm wide.

Internal casts from other bones may also be obtained. The limits of the technique are reached where the cast cannot be removed without considerable damage. This may be the case where numerous canals are involved and especially where the surface layer of the substantia compacta is broken. If the latex penetrates the substantia spongiosa, the bone itself or the cast may be broken in separating the two. The small holes

marking the position of periosteal vessels do not create any difficulty, and are reproduced in a good cast. An internal cast of the sacrum may, for instance, be obtained from a clean, unbroken specimen. That illustrated in figure 2 should be compared with the lead cast illustrated by Lanier and Trotter ('46).

Fig. 1 Internal cranial cast of rubber latex from male Australian Aboriginal skull. Some of the blood vessels have been outlined in white paint. The rough patch in the frontal area is due to insufficient cleaning prior to making the cast. Note the sutures.

The method is being developed further. In particular, experiments are being conducted to find out the reliability of the cast, i.e., what changes in form take place in the course of time.

The casts also lend themselves to the development of a new method of measuring cranial capacity by measurement of their displacement on immersion in water.

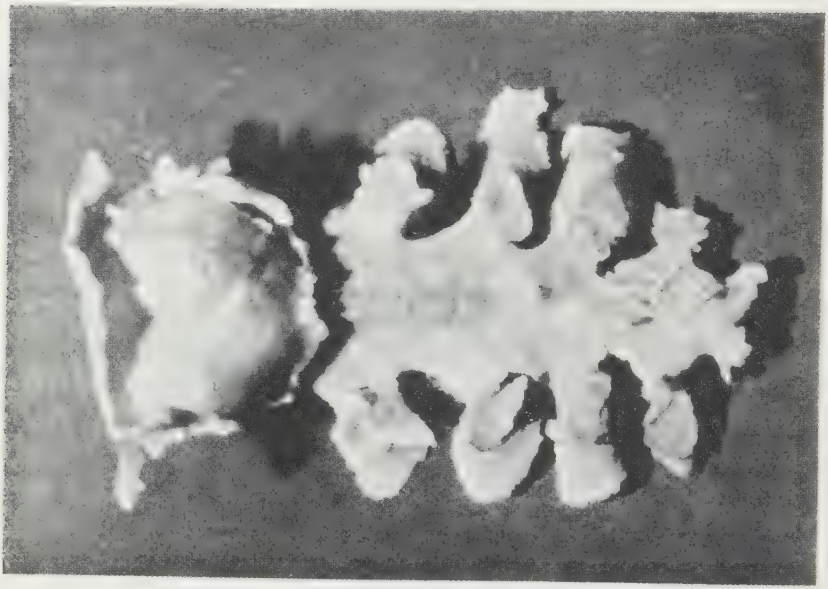

Fig. 2 Internal cast of rubber latex from Australian Aboriginal sacrum. Norma dorsalis.

CONCLUSION

It is possible to obtain internal rubber latex casts of the cranial cavity of primate skulls which are a very close approximation to the form of the cavity. Such casts can be withdrawn through the foramen magnum without damage to the skull. The method may be adapted for use in other spheres where detailed internal casts are required.

Using the latex casts more detailed morphological and comparative studies are possible and, in respect of the skull, the casts lend themselves to the development of a new method of measuring cranial capacity.

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REVIEW

ESSAY ON THE CEREBRAL CORTEX. By Gerhardt von Bonin. Charles C Thomas, Springfield, Ill. 1950. 150 pp.

THE CEREBRAL CORTEX OF MAN. By Wilder Penfield and Theodore Rasmussen. The Macmillan Company, New York, N. Y. 1950. 248 pp.

These two compact little books, appearing in the same year, present current information about the cerebral cortex in entirely different ways. The fact that Penfield and Rasmussen are neurosurgeons, while von Bonin is professor of neuro-anatomy may account somewhat for the diversity in style and content. The physical anthropologist should expect to benefit most from the formal, morphological approach of von Bonin. Yet, it is the reviewer's opinion that the anthropologist will find the neurosurgical account more informative and of greater pragmatic value.

The publishers of the "Essay on the Cerebral Cortex" announce that this book is . . . "written so it might be of interest to both the general reader and the specialist. . . . It endeavors to give that factual information about the cerebral cortex which can be applied to an analysis of its function but to avoid overburdening the reader with a plethora of minutiae." In his preface, the author candidly admits that it will be difficult to cater both to the general reader and the specialist.

von Bonin is an expert in his field. His careful analysis of the cellular arrangement of neuronal patterns in the cerebral cortex is painstakingly done. Yet, by this very thoroughness, the publisher's general claims are often left well out on the proverbial limb. There they are in constant danger of being cut off completely by the author's keen analysis and penetrating attention to minute detail.

Even when the uninitiated is being led by the hand, the going may be disconcerting. For example, the reader may have difficulty working out the firing patterns in the simplified schema of figure 5. The descriptive commentary is too scanty. Labeling the neurons in the figure by numbers would have been helpful. As it is, neuron no. 2 in pattern "a" is never again neuron no. 2 in the other patterns. Nor does neuron no. 3 keep the same identity as the patterns become more complex. There also seems to be some confusion in the basic

assumptions concerning the firing of these units. If one adheres to the conditions stated, it appears that pattern "f" will not fire at all rather than at odd frequencies as stated. The failure to elucidate adequately is a lack that is felt time and again throughout the essay.

One might wish that the author had employed the more familiar Brodmann numbering classification for the cortical areas. The less familiar system of Economo and Koskinas is used throughout, although both Brodmann and Economo maps figure in the text. The specialist, too, might like to question the following unqualified statement on page 85: "The almost universal belief that proprioceptive fibers take course I (i.e. ascend in the posterior columns of the cord) and end in the nucleus gracilis or cuneatus rests on insufficient grounds." No evidence for raising this doubt is given, nor is any evidence to the contrary cited.

Similar tactics of understatement occur in the development of the main theme of the essay which is introduced on page 15 as follows: . . . "the important variable to look for in the brain is not the energy which it consumes, transforms or liberates, but the amount and type of order which it can achieve in the activity of neurons comprising its elements. This is fundamentally a problem of negative entropy. Once it is understood that the problem of the neurologist is a special case of the second and not the first law of thermo-dynamics, many questions concerning cerebral activity can be cast into a much more intelligent form."

This provocative *leit motif* is dropped until page 48, and then its meaning is not clarified satisfactorily. What exactly is negative entropy? What are some familiar examples of its operation? How does the second law of thermo-dynamics differ from the first? Why is the brain a special case of the second law, particularly when one should not be concerned with its energetics? Even specialists in the field of neurology get pretty rusty on matters such as these.

There are moments when the essayist breaks out in a thoroughly engaging style. The reader will be delighted by the Prologue and the introductory chapter and by the sections on sensation, action, prediction and emotion. But the reviewer wonders whether he will be able to follow the Ariadnian thread of the essay through its cyto-architectural labyrinths. The main theme, how the brain handles information, is not woven evenly. It flashes in brilliant design here and there, but it practically fades against the duller webbing of histological detail. In the final chapter where it should sparkle brightly, it is spun gossamer thin, approximating the ethereal. This is undoubtedly a better book for the specialist.

In contrast, "The Cerebral Cortex of Man" by Penfield and Rasmussen can be appreciated by either group of readers. At first blush, it might appear that an exhaustive analysis of over 500 craniotomies in which the cortex of the human brain was stimulated under local anesthesia might make fairly specialized reading. Yet, the material is so interestingly and lucidly presented that even the student of general biology will have difficulty putting the book aside. A considerable bulk of the material is in the form of subjective case reports on the patients as they were being stimulated electrically. But only the pertinent responses have been sifted out, and these are keyed to simplified maps of the exposed cortical areas. Actual photographs of the exposed brain are also shown with the stimulus areas clearly marked by numbered tickets. A functional plan of organization is followed: cortical areas concerned in somato-sensory and somatomotor responses; in autonomic representation; in vocalization and arrest of speech; in vision, hearing and equilibration; in memory, sensory perception and dreams. The localization of these functional regions, and their relationship to each other, is summarized concisely in the final stages of each chapter. The pertinent relationship of these findings to animal studies, lobectomies, lobotomies, and to epileptiform behavior is skillfully woven into the text.

Finally, the last chapter synthesizes the findings discussed under each topical heading, and attempts to relate them into an integrated pattern of cortical function. There are excellent generalized maps of the cortex in this section which do much to bring all of this data into meaningful focus.

The text is an excellent example of concise and lucid writing with a clearly defined organizational pattern always evident. Perhaps, because these authors deal with larger, more readily definable units than does von Bonin, they are able to organize their material with less complexity. But, perhaps, it is because they adhere strictly to facts that their cardinal arguments stand out in bold relief. It is a refreshing and informative book.

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THE PRENATAL ORIGIN OF BEHAVIOR. By Davenport Hooker. University of Kansas Press, Lawrence. 143 pp., 1952. $2.50.— There are two approaches to the study of human fetal activity, and Davenport Hooker is the unquestioned master of the direct experimental method. For 17 years his occasional papers and guest lectures have encompassed the extent of our knowledge of fetal activity, and the development of the behavioral capacities. In this small volume the field of prenatal behavior is summarized, and the findings of Hooker and his co-workers at the University of Pittsburgh Medical School are outlined. The time and sequence of appearance of the various reflexes are given. Moreover, the experimental methods involving saline baths for very immature fetuses, and techniques for non-human fetuses are described in interesting detail. While no attempt is made to relate information based on the tactile stimulation of surgically removed fetuses to the reported behavior of the fetus in utero, "Prenatal Behavior" is a readable account of what has been discovered by Hooker, Coghill, Minkowski, Windle, and others.— S. M. GARN.

TELANTHROPUS AND ITS PHYLOGENETIC SIGNIFICANCE

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FOURTEEN FIGURES

On April 29th, 1949, the author discovered in the Swartkrans excavation the anterior portion of the dental arcade of a mandible which immediately gave the impression of being very different from the mandibles of *Paranthropus crassidens* which had so far been recovered from that site. The following week the remainder of the mandible was discovered. This contained all three molars on the left side and M_2 and M_3 on the right. An isolated P_3 and approximately two inches of the proximal end of a radius were found within a few inches of this mandible. The breccia in this region was poor in bone. The P_3 is worn to a degree exactly comparable with that of the teeth in the mandible. Although there are many general resemblances between this tooth and the *P. crassidens* homologues, this tooth differs so much from the latter that one may be reasonably confident that it belongs to the left side of the mandible. As no other bone was found within feet, in any direction, of these three specimens it is reasonable to consider that the radius fragment also belonged to the same individual as the other two specimens.

At the time these finds were made Broom was engaged on a lecture tour in the United States. On being apprised of the author's discovery and interpretation of these specimens he was most skeptical, but after examining the originals on his return, he agreed that the new specimens represented a more obviously man-like creature than *P. crassidens*. The

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new form was therefore described with the name of *Telanthropus capensis* (Broom and Robinson, '49).

Shortly after the discovery of the above specimens two further finds were made: a fragment of mandible containing M_1 and M_2 and a fragment of snout having only much worn and damaged teeth. The former specimen was briefly described (Broom and Robinson, '50) but not assigned to any genus. It was described as being man-like, contemporaneous with *P. crassidens* and possibly a *Telanthropus* specimen. The fragmentary snout was not developed at the time due to the amount of *P. crassidens* material which was then being obtained. It was considered to be another specimen of *P. crassidens* of which 10 good snouts are known. Recently the author freed this specimen of matrix and was at once aware that it differed considerably from any of the *P. crassidens* specimens now known. The structure of this specimen is such that there can be no reasonable doubt that it belongs with the above mentioned mandible and not to *P. crassidens*. It throws valuable new light on the whole problem, an important point in view of the fact that some workers (e.g. Le Gros Clark, '50) have expressed doubt concerning the correctness of separating *Telanthropus* from *P. crassidens*.

GEOLOGY OF THE DEPOSIT

The geology of the Swartkrans and neighboring sites has been dealt with at some length elsewhere (Robinson, '52b) and will not be considered in detail here. However some geological features must be considered as they have a direct bearing on the correct interpretation of the above specimens.

In the announcement of the discovery of the mandible it was stated that the specimen had been recovered from a pocket of chocolate-colored matrix on the edge of the main mass of pinkish breccia. The conclusion was drawn that *Telanthropus* is more recent than *P. crassidens*.

In a paper describing the fragmentary human mandible (Broom and Robinson, '50) a difficulty was encountered because this mandible was recovered from pink breccia and

was consequently contemporaneous with *P. crassidens.* It was therefore not referred to *Telanthropus* although the possibility was mentioned. In discussing *Telanthropus* in the monograph on the Swartkrans material (Broom and Robinson, '52) Broom assumed that *Telanthropus* is more recent, while the present author expressed the opinion that insufficient evidence was then available to decide whether the material was coeval with or later than *P. crassidens* and its associated fauna.

At the time the above opinion was expressed a fluorine test had been done, through the kind offices of Dr. K. P. Oakley, and this failed to reveal any age difference between the *Telanthropus* mandible and *P. crassidens* material. However this result does not necessarily mean very much. As is well known the australopithecine-bearing breccias are completely consolidated so that excavation has to be done by means of explosives. Once the deposit has become completely consolidated water has less access to the enclosed fossils. At the same time the higher ground was being eroded away and the valleys more deeply incised with the result that the water table must have been appreciably lowered. This would also affect the degree of fluorination as most of the water percolating through the breccia would be surface run-off, which would contain very little fluorine. The rate of uptake of fluorine by the fossils, therefore, must have dropped considerably once the deposit consolidated. The fluorine test was devised for testing fossils in gravel beds through which water passes much more readily. The nature and time of the consolidation process in australopithecine-bearing breccias will naturally have a considerable effect on the conclusions permissible from the above fluorine test. Careful testing of the method under South African conditions seems essential before the meaning of the above result can be assessed with any degree of certainty. According to some recent writers on the subject (Haughton, '48; King, '51) the australopithecines lived in an arid epoch during which wind-blown deposits accumulated, whereas consolidation occurred in a subsequent

wet epoch. According to work by the author (Robinson, '52b) and a detailed geological analysis of these deposits by Brain, at present in progress (Brain and Robinson, abstract in press), the deposits are not primarily of aeolian material but consist of dolomite soil cemented by up to 75% calcite, the consolidation and accumulation processes going on simultaneously. The climatic conditions differed little from those of the present day.

Furthermore the darker patches of breccia were found by Brain to differ only in that less calcite was present as a cementing medium. This probably means that subsequent partial leaching removed some of the calcite which therefore did not so effectively mask the color of the soil. Examples of this leaching of patches of breccia, causing a change in both color and hardness, are common on this site, a fact well demonstrated by Brain's work. In the case of the *Telanthropus* "pocket" the leaching was not marked, as the calcite content had dropped from 70% to 50%. Other examples are known where the calcite content has dropped by several times that amount.

From all of this it is clear that the dark patch of breccia which yielded *Telanthropus* is almost certainly coeval with the lighter parts of the deposit, the different colors being due to differing amounts of contained calcite, not to different age.

Although slight traces of stratification have been found in the australopithecine-bearing breccia at Swartkrans, no evidence has yet been found suggesting that the deposit is not a uniform one: there is no evidence of stratification of the fossils. For example australopithecine remains have been recovered from the surface layers as well as the deepest ones and the characters of the recovered material are very uniform.

(NOTE: Very recent work has shown that an older and a younger breccia exist at Swartkrans but this does not essentially alter what is said here. The "pink" breccia at Swartkrans is a uniform deposit, lithologically and faunally, and contains the australopithecine material. The earlier and later breccias so far have yielded no australopithecine material and are quite distinct, lithologically, from the "pink" breccia.)

While it is clear that in an undisturbed deposit, such as this one, the specimens in the surface levels must be younger than those in the deepest levels, in the case of Swartkrans the time lapse between the bottom and the surface was clearly not great enough for it to be detectable in the contained fauna.

In view of these facts there is manifestly no case for an age difference between the ape-man and the *Telanthropus* specimens. The greatest concentration of *P. crassidens* material was found approximately one-half to two-thirds of the way down from the surface, although the concentration here was not markedly greater than elsewhere. All the *Telanthropus* material was recovered from this same level. The conclusion is therefore clear that *Telanthropus* and *P. crassidens* were strictly coeval as far as the Swartkrans deposit is concerned. The possibility of the *Telanthropus* material being a later burial has been mentioned but can be ruled out at once. There could not be burial into a consolidated deposit. In any case some of the specimens were scattered among *P. crassidens* specimens.

Having established, beyond reasonable doubt, that these two forms are contemporaneous, it would be very useful to establish their absolute age. This is unfortunately less easy to do. However, even here more certainty is now possible than has been the case hitherto. Until the associated faunas of the australopithecine sites have been carefully studied the picture must remain a little obscure. From what is known at the present time it seems likely that the australopithecine-bearing sites, while not all of exactly the same age, are nevertheless of generally similar age.

Stone implements dating back to fairly early in the Pleistocene are relatively common in this area — as in other places in Africa — but nothing which is clearly an artifact has yet been found in any of the australopithecine sites. This suggests that the latest of the sites cannot be as recent as the closing phases of the Lower Pleistocene. Although there are some archaic forms, such as *Lycyaena, Metaschizotherium, Megantereon, Machairodus* and so on, there is a sufficient

admixture of more recent genera to show that an age as far back as Middle Pliocene, suggested by Broom, is unlikely to be correct. On the other hand, although elephants are common in the Vaal River gravels and have even been reported from some of the consolidated breccia deposits of the Sterkfontein area, no trace of them has been found in any of the australopithecine-bearing sites of the Sterkfontein area. No horse remains have been recovered from the Sterkfontein type site (which yielded australopithecine remains) in spite of statements to the contrary by Zuckerman ('50) and Arambourg ('47). Swartkrans has yielded horse remains: *Stylohipparion sp.* and *Equus zebra* which apparently is the same as the Mountain zebra, *E. zebra zebra.* Kromdraai also has several forms of horse, but more advanced forms than has Swartkrans. In this connection it should be remembered that the Kromdraai faunal site, which has yielded most of the Kromdraai fauna, is a short distance away from the small patch of breccia which yielded the australopithecine specimens. No positive proof is at present available showing the exact age relationship of these two deposits but there is nothing in the known evidence which precludes their being the same age.

Some authors have attempted to correlate the Vaal River climatic curve with the evidence available from the australopithecine deposits. Cooke ('47), Haughton ('48) and King ('51) are all in agreement that the australopithecines lived in an arid epoch in which extensive deposits of wind-blown sand accumulated. These deposits were then consolidated in a later wet phase to form the australopithecine-bearing breccias. Cooke ('47) considers this epoch to be coeval with the arid phase separating his Older Pluvial from the Younger Pluvial of the Vaal River basin climatic sequence. However Pre-Stellenbosch implements are already present before the close of the Older Pluvial. Now it seems reasonable to suppose that traces of this culture should be found *somewhere* in these deposits if they post-dated the arrival of the people responsible for these tools. But no such traces have been

found in spite of much searching. Furthermore recent work (Robinson, '52b and work still in progress by Brain) shows clearly that the australopithecine-bearing breccia at Swartkrans is not a primarily aeolian deposit but consists of fossilized soil of the period of accumulation. This soil differs very little from the modern soil of the area. To speak of this epoch as being arid and Kalahari-like is therefore not correct. From the recent studies it seems that the climate of the time was fluctuating slightly about a condition very similar to that obtaining in this area today. There appears to be a trend towards slightly moister conditions in the main body of breccia and so if this deposit is to be fitted into the Vaal River curve it should presumably fit into early stages of either of the pluvials. Both from cultural and faunal points of view the Younger Pluvial is too recent. Placing the site in the early part of the Older Pluvial would make it late Upper Pliocene, according to Cooke's curve. However this presupposes that the said curve is correct both as regards climatic changes and dating. The "aeolian red sands" of the Vaal River therefore need careful study in the light of the investigations on the Swartkrans australopithecine breccias. Furthermore it is not yet certain whether the climatic trends observed in the australopithecine breccias are minor variations or are comparable with the supposed pluvials of the Vaal River sequence. The correlation between the australopithecine-breccia studies and those of the Vaal River basin should therefore be accepted only with caution until the doubtful points are cleared up.

In view of all this it seems that the age of the australopithecine period, in the Sterkfontein area, can be stated with a considerable degree of certainty to be from late Upper Pliocene to late Villafranchian (Kageran). It also seems clear that the order of decreasing age is: Sterkfontein, Swartkrans and Kromdraai. The absolute age of Swartkrans is therefore not certain. In some respects it seems to be quite close to Sterkfontein in age. If one takes the age of Swart-

krans as a million years in round figures (Plio-Pleistocene junction) the percentage error will not be large.

THE NEW TELANTHROPUS SPECIMEN

As will appear later in this paper, the group of specimens referred to in the introduction all appear to belong to *Telanthropus capensis*. The type mandible has been described (Broom and Robinson, '49, '52) and also the mandibular fragment (Broom and Robinson, '50). The newly cleaned

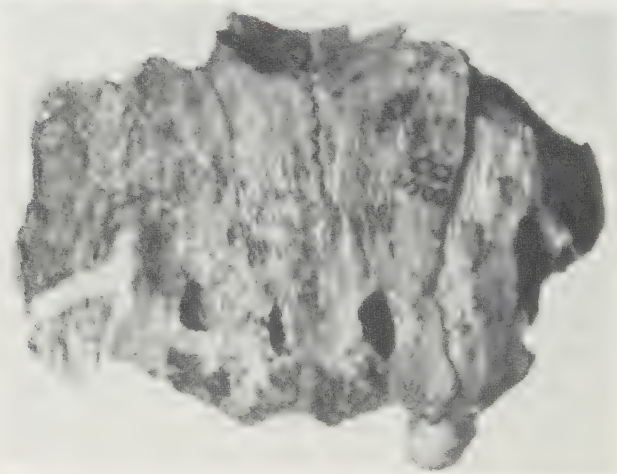

Fig. 1 *Telanthropus* III maxillary fragment in anterior view. Approximately × 1.5.

maxillary fragment will be described in detail after which the specimens will be considered as a whole.

As will be clear from the photographs in figures 1, 2 and 3, this specimen is unfortunately fragmentary. The alveolar margin is present almost intact between, and including, the canine sockets. In the midline the palate is present to approximately the position of M^1. The alveolar portions on either side are incomplete posterior to the canine sockets. The greater portion of the subnasal plane of the maxillae is present, extending from the midline to the region of P^3 on either side. Part of the floor of the nasal cavity is present

from the anterior nasal spine to a short way behind the incisive foramina.

The teeth are very worn and only a few are present. The left lateral incisor is present, half out of its socket, but attrition has reached such an advanced state that the crown has been worn down almost to the cervical line on the buccal and lingual aspects. Portions of the roots of right and left P^3 are present as well as a portion of the root and crown of what is probably the right P^4. The lingual root of the

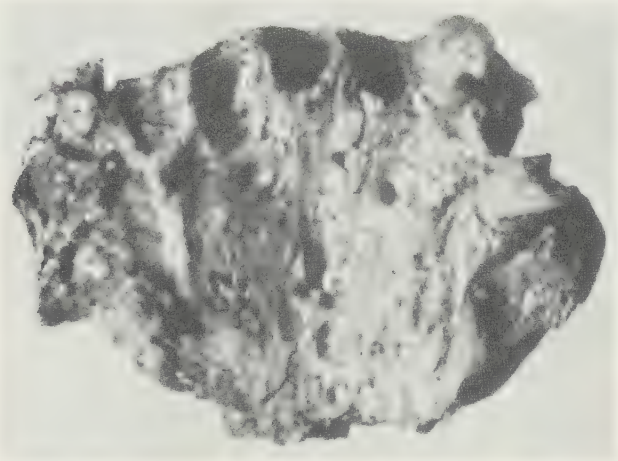

Fig. 2 *Telanthropus* III maxillary fragment in palatal view. Approximately × 1.5.

right P^3 as well as the fragment of P^4 are not in their respective sockets but were loose in the matrix occupying the region of these sockets.

Because of the extreme degree of attrition and the fragmentary nature of the teeth present, comparatively little can be said about them. The broken, presumed P^4 has a small pulp cavity. The canine roots are not preserved but both sockets are. That on the left side has the buccal wall missing, hence the whole length may be studied. The socket length, measured from the alveolar margin between I^2 and C^-, is 19.8 mm.

Unfortunately only one corresponding socket of *Paranthropus crassidens* can be measured and this is 27 mm in length. An isolated upper canine of the same species with an intact root has a root length of 27.5 mm. According to Shaw ('31) the average length of the root in the Bantu is 17.3 mm. However, socket lengths of 18 or 19 mm are not infrequent. Campbell ('25) gives the average root length of the maxillary canine root of the Australian aboriginal as 19.9 mm. Socket lengths equal to that of the *Telanthropus* specimen should therefore be much more common among this group than among the Bantu. This *Telanthropus* specimen thus has upper canine roots appreciably shorter than those usual in *P. crassidens* but only slightly longer than those usual in modern man. The maximum mesiodistal and buccolingual dimensions of the *Telanthropus* socket are respectively 7.3 mm and 9.5 mm. The only intact root of *P. crassidens* has the corresponding dimensions of 8.2 mm and 10.7 mm. The *Telanthropus* specimen consequently had an upper canine root smaller in every respect than the only intact homologue of *P. crassidens*. In this respect it should be borne in mind that the latter form has very small-crowned incisors and canines compared to the postcanine teeth.

Although no completely intact roots of P^3 are present in the *Telanthropus* specimen it is quite clear from the sockets on the right side that P^3 had three separate roots, the mesiobuccal one being closely approximated to the canine root. The situation on the left side is less plain but at least two, and probably three, roots were present. The lingual root is *in situ*. In *P. crassidens* three roots are also present but in some cases the mesiobuccal root is almost completely fused with the lingual one.

The palate exhibits a number of points of interest. The incisive fossa is of moderate size and is smaller than that of *P. crassidens*. It appears to be situated further back than that of the latter form but this is not really the case. The position relative to the tooth row is the same and the actual distance, measured in the plane passing through the alveolar

margin, is also the same. Due to the considerably greater depth of the *Telanthropus* palate, however, the oblique distance from the fossa itself to the alveolar point is here greater. The actual opening of the incisive fossa is narrow and from it two clearly defined but low ridges diverge forward, each running directly to the center of the posterior margin of an I^1 alveolus. The bone surface between these two lines is moderately concave. The condition is much the same as that found in modern man — and *Pithecanthropus* to judge from illustrations — except that in modern man the fossa is situated very slightly more anteriorly. In *P. crassidens* the fossa is wider and has a thickened border on either side. These also pass forward, diverging slightly, but about half way to the alveolar margin these borders turn sharply away from the midline. Where this lateral swing occurs the remainder of the suture between the maxilla and premaxilla can usually be found. These features are to be seen in all (6) of the palates of *P. crassidens* where this region is not damaged. In the *Telanthropus* specimen the right incisive canal is smaller than the left one, a condition also found in the *Pithecanthropus* palate and frequently in modern man.

Unlike the condition common in *P. crassidens,* the palatal midline just posterior to the incisive foramen is not raised into a small torus but is instead very slightly depressed. Five oval depressions, three on the left side and two on the right, occur immediately on either side of the suture separating the two maxillae. The anterior one on the left side is small but the others are all between 3 and 4 mm in length and about 1 mm in depth. The author has never observed similar structures as well developed anywhere else. Traces of similar depressions are visible in some specimens of *P. crassidens* (SK.12, for example) and also in some specimens of subfossil Bush skulls. These depressions were presumably made by palatal glands. Three relatively large foramina are present in the palate anterior to the incisive foramen. These also are larger than any observed by the present writer elsewhere. Several *P. crassidens* specimens show smaller

examples of similar foramina. Foramina of the same sort are also occasionally encountered in modern man.

Because of the width across the neck of P^3 and the obvious smallness of the canine, the palatal margin of the canine socket is slightly recessed between the I^2 socket and that of the lingual root of P^3. This feature is common in *P crassidens.*

From the palatal aspect this specimen differs from *P. crassidens* primarily in the relatively great depth of the palate anteriorly, the shallow canine socket and the different size

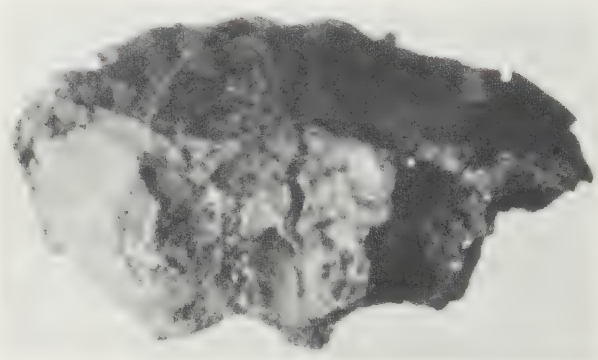

Fig. 3 *Telanthropus* III maxillary fragment seen from above. Approximately × 1.5.

and conformation of the incisive fossa and its immediate surroundings. The three enlarged foramina and the depressions along the midline are probably very variable features.

Turning now to the external surface: the distance from the anterior nasal spine to the alveolar point is 33 mm. This is essentially the same as the corresponding distance in *P. crassidens.* From the base of the pyriform aperture to the alveolar margin the subnasal plane or surface is relatively flat and wide. The midline, along the intermaxillary suture, is slightly raised and the surface slopes gently to either side to the slight canine eminences. In strict side view the midline and the nasal spine can easily be seen. This is not the case in *P. crassidens* in which the canine roots — hence the

canine eminences — are robust and the region between them is depressed. Consequently in true side view neither the midline nor the anterior nasal spine are visible. This depression, which is usually not present near the alveolar margin where the I^1 roots cause a double eminence, is characteristic of all the *P. crassidens* specimens, in some cases (SK.12) markedly so. Furthermore the anterior nasal spine is situated relatively far back in the floor of the external nasal aperture and there is no clear demarcation of the lower margin of the aperture. The subnasal plane passes smoothly

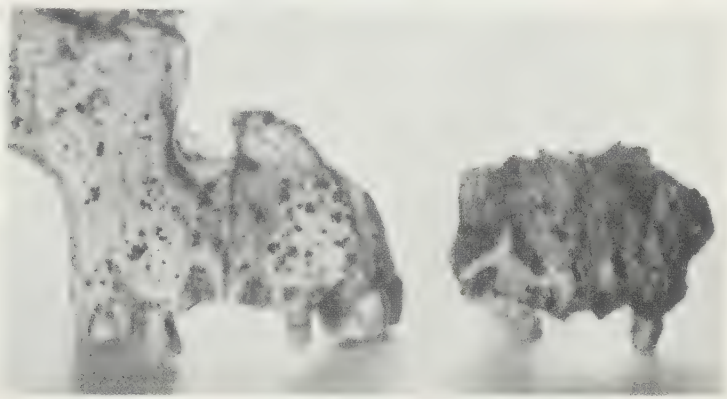

Fig 4 Comparison of *Telanthropus* III with the corresponding portion of a skull of *P. crassidens* (SK.52).

and quite insensibly into the nasal cavity. In *Telanthropus* the anterior nasal "spine" is only a slightly raised, roughened region but it can easily be seen in lateral view and the lower margin of the pyriform aperture is very clearly defined. The surface of the small bony platform immediately inside the nasal cavity is approximately at right angles to the surface of the subnasal plane and the two are separated by a small ridge running to either side from the anterior nasal spine. Posterior to the latter there is no raised trough to accept the septal cartilage. The bony "platform" just inside the nasal cavity not only has a well defined anterior edge but also a posterior edge. In the midline this posterior edge is

produced into a spine. In the space between the two halves of the spine a small slip of bone is inserted which appears to be the anterior tip of the vomer. Back of this posterior edge, on either side of the spine the bone projects backwards, at a slightly lower level, for a short distance before curving down into the relatively large incisive foramina. These foramina are about as large as are those of *P. crassidens* and of *Pithecanthropus* IV. *Telanthropus* has a small but definite

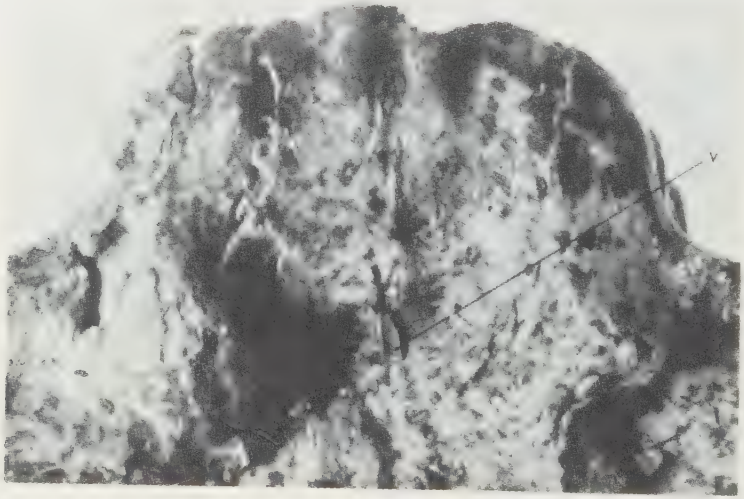

Fig. 5 The snout of a specimen of *P. crassidens* (SK.79) in dorsal view showing the vomer inserting against the back of the anterior nasal spine. Slightly larger than life size.

anterior nasal spine which is separated by a centimeter from the posterior end of the incisor crest and the upper openings of the incisive canals. The anterior point of the vomer meets the maxillae between the upper openings of the incisive canals and hence is also a centimeter from the anterior nasal spine. The condition in modern man is very similar except that the distance from the anterior nasal spine to the posterior end of the incisor crest is often a little more than a centimeter as the nasal spine is commonly well developed. In skulls where the nasal spine is poorly developed, as it is

in the *Telanthropus* specimen, this distance agrees very well with that in the latter form. In *P. crassidens* the situation is very different because the vomer actually inserts against the back of the anterior nasal spine. This can be seen very clearly in SK.52 where the vomer is still in position and is continuous with the back of the spine. The incisive canals open immediately behind the spine, on either side of the anterior end of the vomer. This situation is present in all of the *P. crassidens* specimens in which this region is preserved. It is especially clear in SK.52, 46 and 79. In *Plesianthropus* the condition of this region is very much as in *P. crassidens* but the two are not identical. Of 4 specimens of *Plesianthropus* three have a slight separation between the spine and the anterior end of the vomer (varying from about 2–5 mm) while the other has no separation at all. But even in the skull with the greatest separation (No. 5) there is still very little resemblance to the condition found in *Telanthropus* because the separation of the spine from the anterior end of the vomer is not horizontal but almost vertical. In other words the vomer meets the maxillae appreciably lower down in *Plesianthropus* than it does in *P. crassidens*.

There is, therefore, a clear distinction between *Plesianthropus* and *P. crassidens* on the one hand and *Telanthropus* on the other. The *Plesianthropus* condition is perhaps more likely as a precursor of that of *Telanthropus*. The homologous region is not adequately preserved in any adults of the other australopithecines.

The zygomatic and frontal processes of the maxillae are missing. From the conformation in the immediate neighborhood of the lower portion of the nasal aperture it seems probable that the bone surface on either side of the anterior nasal aperture was directed more nearly vertically than is the subnasal plane. The appearance of this general region must have been very similar to that in *Pithecanthropus* IV. If this is the case there must have been a more definite projection of the nose in *Telanthropus* than is the case in *P. crassidens*.

The most telling differences between the *Telanthropus* specimen and *P. crassidens* are therefore to be found in the lower portion of the nasal cavity and its immediate surroundings. As in the case of the type mandible there may

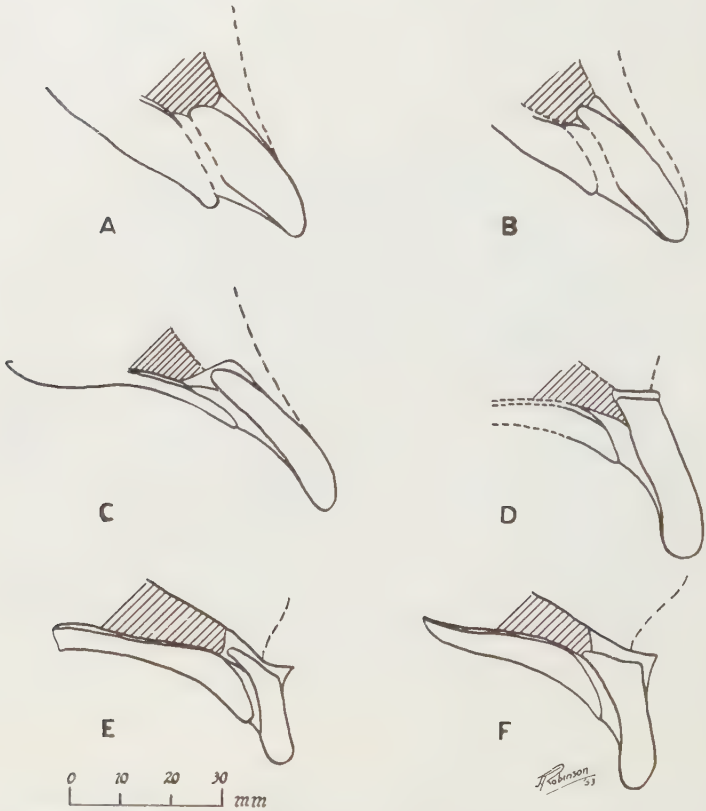

Fig. 6 Sagittal sections through the snouts of A-B, *P. crassidens;* C, *Plesianthropus;* D, *Telanthropus* III; E-F, *Homo* (Bush). As well as the strictly sagittal section, the structure immediately to one side is also shown. The shaded portions represent the anterior end of the vomer in each case.

be some who will be inclined to regard this specimen as an extreme variant. Ten *P. crassidens* specimens with this region preserved are available for comparison. Morphologically these are remarkably uniform, the most obvious difference being in the width of the pyriform aperture which varies

from 18 mm (SK.13) to 29 mm (SK.11). The degree of depression of the region of the anterior nasal spine is also variable. There is nevertheless marked uniformity and *all* contrast sharply with *Telanthropus* in respect of the above differences; there are no intermediate forms. Precisely in those characters in which the latter form differs from *P. crassidens* it closely approaches the euhominid condition (see fig. 6). Due to the shape of the anterior nasal spine the difference between *Telanthropus* and the australopithecines is minimized in median sagittal sections. In the figure, therefore, the mid-sagittal section is combined with a section a few millimeters to one side of the midline to bring out more fully the real differences. There are two chief differences between the sections of *P. crassidens* and *Plesianthropus:* the former has a shallower palate and the bone is much more robust. The *Plesianthropus* 5 skull is also considerably more prognathous but two other skulls of the same type are not as markedly so. However in the sections of both australopithecines the same features are found: relatively shallow palate, depressed floor of the nasal cavity, lack of differentiation between nasal cavity floor and subnasal plane and finally the small angle between the subnasal plane and the Frankfort plane. There is an appreciable difference between man and the australopithecines in respect of each of these features. Each of the corresponding features of the *Telanthropus* specimen is of the euhominid type. It is not necessary to stress the fact that in so widespread and complex a group as modern man there is a good deal of variation in the lower half of the face. In spite of this variation the author has never seen a skull of modern man exhibiting the characteristically australopithecine features here discussed. In some cases the palate is very shallow, the prognathism marked, or the distinction between the floor of the nasal cavity and the subnasal region blurred, but nevertheless the complex of characters is always clearly human. This essentially euhominid appearance is also found in *Pithecanthropus* IV and *Telanthropus*.

In the specimens of *Paranthropus robustus* and *Australopithecus prometheus* the midline is not preserved in the relevant region. However enough is present to show that these forms also had typically australopithecine characters as described above.

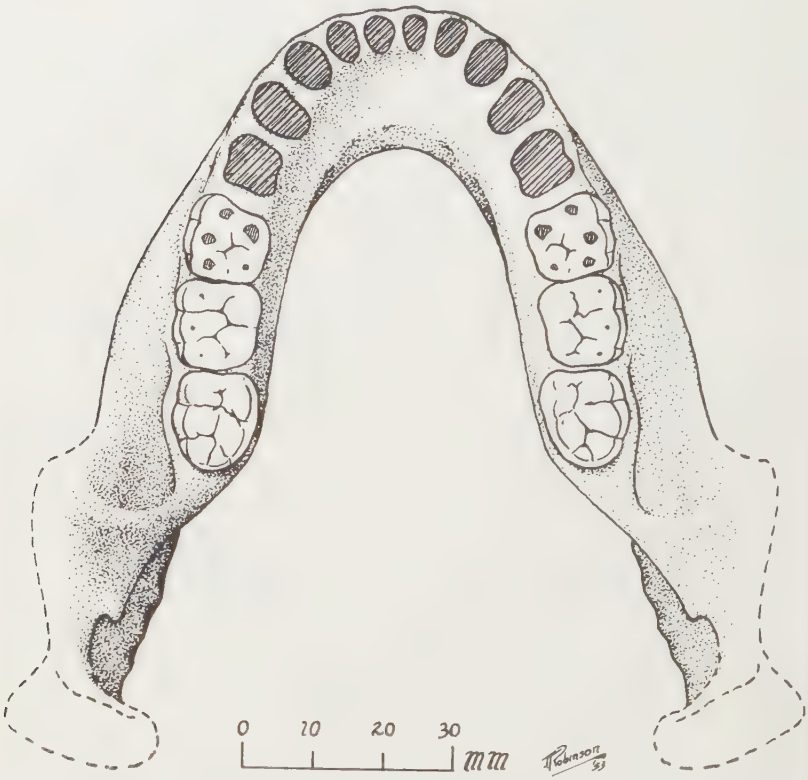

Fig. 7 *Telanthropus* I (type) mandible, slightly restored. Natural size.

THE TYPE MANDIBLE

The *Telanthropus* type mandible has been described in some detail (Broom and Robinson, '49, '52). It will therefore not be described again here but some salient features will be discussed. A graphic reconstruction is here given (fig. 7) of this mandible. This differs in some respects from that

of Broom (in Broom and Robinson, '52). Although the mandible is almost complete — it has only 5 molars *in situ* but otherwise only the coronoid processes and condyles are missing — there has been an appreciable amount of cracking and distortion. However the reconstruction here given cannot depart from the truth by more than a very small margin in any particular feature. The chief difference between Broom's reconstruction and the present one is the slightly greater massiveness of the former. This is due to insufficient allowance by Broom for expansion of the bone due to cracks being filled with matrix.

TABLE 1

All dimensions are in millimeters

DIMENSION	TELANTHROPUS	P. CRASSIDENS (SK.23)
Maximum length	109.0	127.0
Bicondylar width	114.0	117.0
Body height at canine	31.5	40.0
Body height at M_3	25.0	33.0
Ramus height at coronoid	59.0	91.0
Ramus height at condyle	55.0	84.0
Maximum corpus width at M_2	22.5	25.0

One other reconstruction of this mandible should be mentioned — that by Weinert ('52). This reconstruction bears comparatively little resemblance to the original. This is perhaps understandable as it was done from a photograph only. In particular the relative narrowness of the jaw as reconstructed by Weinert — a fact to which he draws attention as being a somewhat pongid feature — is incorrect. The mandible is in fact wider than it is long. As reconstructed by the author the maximum length, measured in the midline, is 109 mm, while the bicondylar width is 114 mm. Both these values are naturally not exact as both condyles are missing and the size and shape of the condyles will affect both values to a small extent. The condyles have been here reconstructed along the lines of those of *P. crassidens*, which are more like

those common among modern euhominids than are those of the Mauer and La Chapelle mandibles, for example.

This mandible is notable for the lowness of the corpus mandibulae and the ascending ramus. The corpus height at the position of the canine is 31.5 mm and at M_3 25.0 mm. The ascending ramus, as preserved on the left side, is 46 mm in height. As reconstructed the height at the coronoid process is 59 mm, and 55 mm at the condyle. Although both condyles are missing, on the right side the break has occurred at a point where the ramus is rapidly thickening just below the condyle. On the left side the break has occurred in the same position but the impression of a good deal of the condyle is preserved in the adjacent matrix. Consequently the position, but not the size and shape, of the condyle is known within narrow limits.

In table 1 comparison is made between the *Telanthropus* mandible and mandible SK.23 of *P. crassidens*. The latter is almost perfect insofar as practically nothing is missing and there is only a very slight amount of distortion. It appears to agree very well in size with the other, more fragmentary mandibles of *P. crassidens* but is not the largest specimen. Maximum length is measured in the sagittal plane. SK.34, which also has an intact ascending ramus, has the height at the coronoid process of 105 mm. In this specimen the corpus width at M_2 is equal to that in *Telanthropus* but in SK.12 this measurement is 34 mm.

The *Telanthropus* mandible is appreciably smaller than that of *P. crassidens* and also differs in many proportions, e.g., the bicondylar width is greater than the maximum length and the corpus and ramus heights are relatively low. In *P. crassidens* the length exceeds the bicondylar width and the antero-posterior dimension of the ramus of SK.23, at the level of the tooth row, exceeds that of *Telanthropus* by only 6 mm but the ramus heights differ by 32 mm.

In *Telanthropus* the maximum antero-posterior diameter of the symphysis is 16.0 mm while in *P. crassidens* it is 24.5 mm in SK.23 and 27.8 mm in SK.12. This means that in

P. crassidens the symphysis extends further back and, as the body thickness in this region is relatively great, the inner contour in a horizontal plane is more nearly "V" shaped than "U" shaped. In *Telanthropus* this is not the case. There the inner contour in back of the symphysis is parabolic with a relatively wide space between the two halves of the jaw

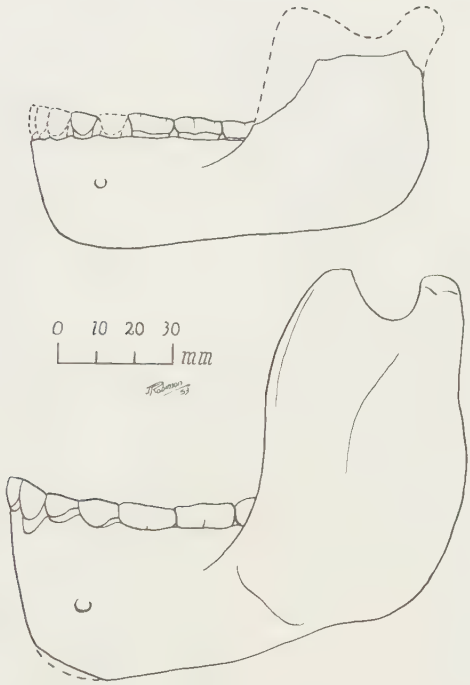

Fig. 8 Lateral view of the *Telanthropus* I mandible compared with that of *P. crassidens* (SK.23).

— in fact the normal euhominid condition. This is clearly shown by the fact that the minimum internal distance between the two halves of the mandible, measured at the position of M_1, is less than the labiolingual diameter of the corpus mandibulae at that point, in all the adult mandibles of *P. crassidens*. In the *Telanthropus* mandible the reverse is the case: the internal measurement is almost double the corpus width.

In sagittal section the symphysis of the *Telanthropus* mandible differs a little from any of *P. crassidens* now known, although the similarity is considerable. The chief difference, besides the much greater massiveness of the latter, lies in the fact that the protuberance immediately below the genioglossal fossa is poorly developed in *Telanthropus*. The genioglossal fossa itself is also less clearly defined than is the case in *P. crassidens* and *Meganthropus*. In euhominids this fossa is not usually well defined and commonly the greatest lingual protuberance of the symphysis is immediately below the fossa. This lower protuberance or inferior transverse torus is usually confined to the region of the midline and the general region around the lower portion of the symphysis, lingually, slopes downward and forward under the chin. However the protuberance below the genioglossal fossa is not always the most prominent. In some cases the reverse is true. One Korana mandible in our collection has a symphysis not unlike that of *Telanthropus,* except for the much better developed chin of the former. Among the *Sinanthropus* mandibles are some whose lingual half of a symphyseal section is even more like that of *Telanthropus*. The latter apparently has no clearly defined mental protuberance. In at least one *P. crassidens* mandible there is a well defined mental protuberance. In general this form appears to have a more nearly vertical anterior face in the midline and, in one case, better developed mental protuberance than has *Telanthropus*. The latter therefore approaches the euhominids more closely than *P. crassidens* in respect of the considerably less massive symphyseal region and the structure of the lingual portion of this region but is a little less euhominid in the structure of the external portion of the symphysis.

Lateral and postero-lateral to the third molar, anterior to the torus triangularis and medial to the anterior portion of the ramus is a relatively large retromolar fossa. This fossa is wide but not deep. The retromolar fossa in *P. crassidens* is much larger and is excavated below the level of the crista pharyngea — in SK.23 well below it. In the latter form the

crista endocoronoidea, the crista endocondyloidea and the planum triangularis are well defined, the surface of the latter being well below the two cristae, i.e. the two cristae are prominent ridges on the medial surface of the ramus. The crista

Fig. 9 *Telanthropus* I mandible. Approximately natural size.

endocoronoidea is normally more clearly defined than the other.

In *Telanthropus* the appropriate region is not preserved in its entirety but what remains of it shows clearly that only the crista endocoronoidea is at all clearly defined and that

only because it has a prominent anterior margin due to the well developed retromolar fossa.

As in *P. crassidens* M_3 is largely obscured by the ramus in *Telanthropus* when the mandible is seen in lateral view.

The mandibular foramen and mylohyoid groove differ in *Telanthropus* and *P. crassidens,* the condition in the former being more nearly like that common in modern euhominids. Some misunderstanding probably exists in this connection as a consequence of a statement made in the announcement of the discovery of *Telanthropus* (Broom and Robinson, '49) and subsequent comment by Straus ('50). Let it be admitted at once that the statement to which Straus objected ("The typically human mylohyoid groove in our supposed man, and the certainly not typically human groove in *Paranthropus,* seems to make it certain that the two jaws belong to different genera") is not acceptable as it stands. We had only a small collection of pongid skulls for comparison and as it so happens every one (including specimens of all the living forms) has the so-called "simian type" of groove. This completely supported the statements of Keith and Friedrichs and we therefore accepted them. However Straus gives the impression that our diagnosis turned completely round this one point by saying that "this relationship was evidently a decisive factor in leading Broom and Robinson to regard their new specimen as belonging to a genus wholly different from *Paranthropus*" without mentioning any of the other differences which had been cited. Although the original passage is admittedly badly worded it nevertheless seems clear, on reading the whole note, that this point was regarded as strongly confirmatory evidence for a conclusion based primarily on the general size, shape and proportions of the mandible and the size and structure of the molars. These other features all suggested a creature different from, and more euhominid than, *P. crassidens.* The mylohyoid groove evidence seemed to underline that conclusion.

Subsequently it appeared that the statement that *P. crassidens* has a "simian type" of groove is incorrect. The only

mandible in which the appropriate region is preserved, then available (SK.12), has only the lower portion of the groove clearly marked. This portion is so situated that an upward extension in the same direction would take it well behind the mandibular foramen. Subsequent specimens all have the groove well marked all the way and show that in no case does the groove terminate wide of the foramen. In fact the so-called "simian type" is not present in any australopithecine specimen known at the present time. Careful examination of even the SK.12 mandible with strong side light shows a faint groove joining the foramen to the more clearly defined portion of the groove. All the *P. crassidens* specimens therefore have the "human type" of groove. So has *Telanthropus* but there is nevertheless a clear distinction between the groove and mandibular foramen in this specimen and in *P. crassidens*. In the latter form the mandibular foramen is comparatively small and has only slight traces of a lingula. The mylohyoid groove leaves the foramen approximately centrally on the lower border. In *Telanthropus* there is a clearly defined lingula, of which the tip is broken off. The lower margin is not elongated antero-posteriorly as in *P. crassidens* but is elongated downward slightly and from the lowest point the mylohyoid groove commences. Although both foramen-and-groove complexes are of the so-called "human type," examination of the extensive collection of human skulls here and at the Anatomy Department of the University of the Witwatersrand suggest that the *Telanthropus* condition is more nearly typical of modern euhominids than is the *P. crassidens* type. In *Plesianthropus* the condition is more nearly like that in *Telanthropus*.

Straus points out that the type here described for *Telanthropus* is "the most characteristic hominid variant of the 'human' type" and is possibly more diagnostic of euhominids. He goes on to say, "But even this fails as a truly distinctive human character, for it is almost as common in the baboon as in man and not at all uncommon in the gibbon and gorilla." However the fact that *only* the most characteristic hominid

variant is known in the australopithecines and *Telanthropus* is surely of considerable significance. It seems improbable that one should find oneself in a position where it is almost impossible to distinguish between a baboon and a man, and should one find oneself in so parlous a condition it is unlikely that one could turn to the mylohyoid groove to extricate oneself. The mylohyoid groove was, and is here, used at a

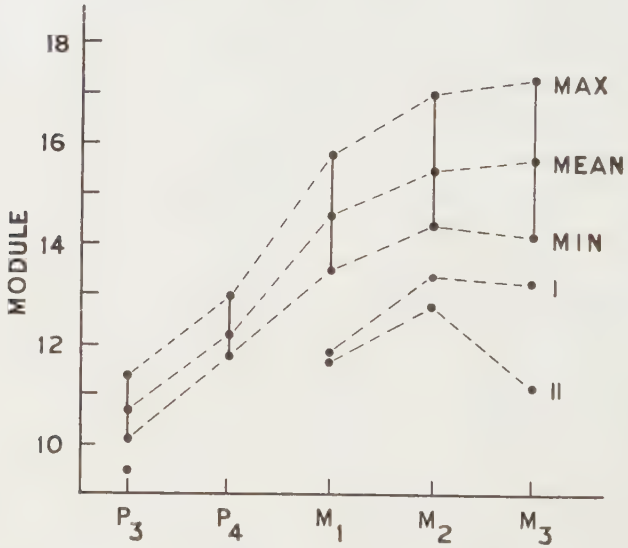

Fig. 10 Comparison of maximum, mean and minimum modules for P_3–M_3 of *P. crassidens* with the modules for P_3, M_1–M_3 of *Telanthropus* I and those for M_1–M_3 of *Telanthropus* II. In the case of *P. crassidens* the ranges here given are based on the following number of specimens: P_3, 8; P_4, 7; M_1, 13; M_2, 10 and M_3, 14.

different level of significance from that in which Straus used it. The information he has provided is of considerable interest but the chief point about the mylohyoid groove and mandibular foramen type of *Telanthropus* is that it is *different* from that in any of the *P. crassidens* specimens. In view of the fact that *Telanthropus* and *P. crassidens* are coeval and from the same excavation, the former is either a different creature or it is a member of the same local population as

the latter. This gives the differences between the two forms greater significance than if *Telanthropus* had come from a separate site because there are no specimens from this site which link the relatively uniform *P. crassidens* characters with those of *Telanthropus*.

The teeth in this mandible have been described at some length by the author (in Broom and Robinson, '52) and only the main features will here be dealt with.

All of the teeth (P_3, M_1, M_2 and M_3) are appreciably smaller than those of *P. crassidens*. The dimensions (in millimeters)

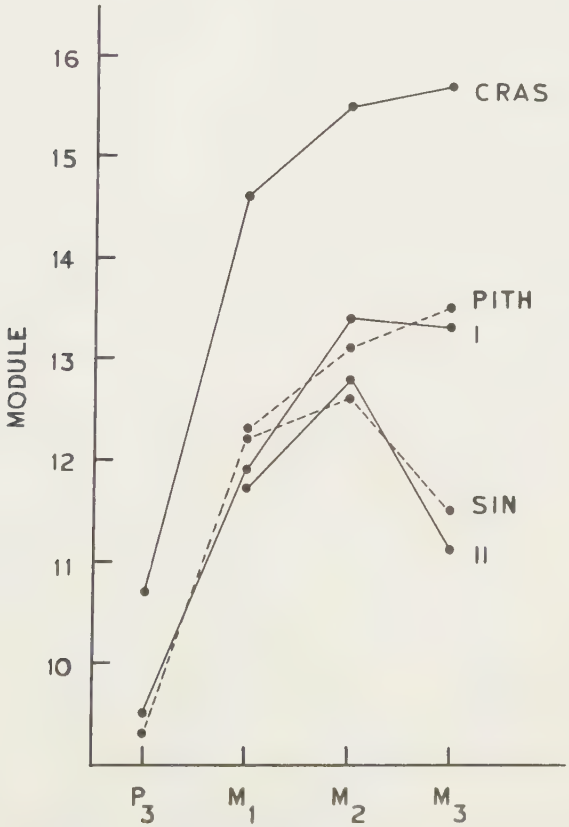

Fig. 11 Comparison of the modules of P_3 and M_1–M_3 of CRAS, *P. crassidens* mean; PITH, *Pithecanthropus* B; I, *Telanthropus* I; SIN, *Sinanthropus* (mean) and II, *Telanthropus* II.

TABLE 2

All dimensions are in millimeters. L = mesiodistal length. B = buccolingual breadth. M = module

	P_3			M_1			M_2			M_3		
	L	B	M	L	B	M	L	B	M	L	B	M
P. crassidens (Robinson)	9.7	11.7	10.7	15.0	14.3	14.7	16.0	15.0	15.5	17.4	14.5	16.0
Telanthropus (Robinson)	8.6	10.3	9.5	11.9	11.9	11.9	13.6	13.1	13.4	14.1	12.4	13.3
Pithecanthropus (v. Koenigswald)	..	..	..	12.5	13.0	12.3	13.0	13.2	13.1	14.5	12.5	13.5
Sinanthropus (Weidenreich)	8.7	9.9	9.3	12.6	11.8	12.2	12.6	12.6	12.6	11.7	11.2	11.5
Australian (Campbell)	7.6	8.8	8.2	12.3	11.9	12.1	12.5	11.7	12.1	11.9	11.1	11.5
Bantu (Shaw)	7.1	8.2	7.7	11.0	10.5	10.8	11.0	10.3	10.7	11.1	10.4	10.8
American Whites (Black)	6.9	7.7	7.3	11.2	10.3	10.8	10.7	10.1	10.4	10.7	9.8	10.3

of these teeth are given in table 2, along with the dimensions of corresponding teeth of other forms for comparison. It will be seen that the dimensions of the *Telanthropus* teeth agree very well with those of the early euhominids. M_1 of *Telanthropus* is exceeded by that of the modern Australian aboriginal. On the other hand there is a clear separation between the sizes of the *Telanthropus* teeth and the minimum values for *P. crassidens*. There is greater size difference between the first molars of these two forms than between any of the other teeth. In mesiodistal length the *Telanthropus* tooth falls 5.4 times the standard deviation from the mean for *P. crassidens* and the buccolingual breadth 3.8 times the standard deviation. The latter figure is highly significant and the former very highly so. The size difference in the case of the other teeth is only just significant or not quite significant depending on the level of significance adopted. Attention is here directed to the fact that the *Telanthropus* M_1 is considerably worn as all 5 cusps are worn through to the dentin. The maximum buccolingual width will be negligibly affected by this wear as even in this stage of wear the occlusal width is less than the maximum width. But the mesiodistal length (measured in the midline of the tooth) will be appreciably affected. The figure here used (11.9 mm) is almost a millimeter and a half greater than the actual measurement, so that the wear has been allowed for. As the size difference is so significant in the case of this tooth the smaller degree of difference in the case of the other teeth is of little consequence as they all belong in the same mandible. If M_1 cannot belong to the *P. crassidens* group neither can the rest of the mandible.

It is of interest to note that in *Telanthropus* M_3 is smaller than M_2 but this is not the case in *P. crassidens*. There is one exception to this: in the *P. crassidens* mandible SK.23 M_3 on the left side is a little smaller than that on the right. The module (and the robustness index) of M_3 on the right side is appreciably larger than that of the right M_2, while that of the left M_3 is slightly smaller than that of the left M_2. However, if the average dimensions for M_3 are compared

with those of M_2, in this mandible, M_3 is still noticeably larger than M_2. *P. crassidens* and the *Pithecanthropus* B mandible have M_3 larger than M_2. The Bantu is of interest in that the average figures (as given by Shaw, '31) are almost exactly the same for all three molars, with M_2 very slightly smaller than the others. *Sinanthropus,* although a very early euhominid, has M_3 strongly reduced — more so than in living forms, on the average.

Apart from differences of size and proportion, morphological differences are apparent between the teeth of *Telanthropus* and those of *P. crassidens.*

Except for the smaller size, P_3 of *Telanthropus* is very similar to that of *P. crassidens.* The distolingual angle of the crown is produced, the lingual cusp is rotated mesialward and the posterior fovea is much larger than the anterior one, as is the case in *P. crassidens.* However, when seen in buccal view, the crown of the *Telanthropus* tooth is appreciably narrower at the cervical line than it is at the occlusal surface. This is not the case in *P. crassidens.* The root system of the *Telanthropus* tooth tapers downward when viewed from any side while that of *P. crassidens* is wider at the apex, in mesial or distal view, than it is at the cervical line. In these two features *Telanthropus* approaches the characteristic modern euhominid condition more closely than does the other form. This is also true of root length. The greatest length of the root, measured on the mesial face, is 13.9 mm in *Telanthropus* whereas in *P. crassidens* the corresponding measurement is in all known cases greater than 20 mm, the average being 20.5 mm. Black gives the average length of this root in American Whites as 14 mm. The author has elsewhere ('52) shown that the known characters of the australopithecine and euhominid P_3 roots can very easily and convincingly be fitted into a single evolutionary series starting from a double-rooted form in the early australopithecines to the single-rooted form characteristic of modern euhominids. The true double-rooted form was not known at the time but was put forward as an hypothetical ancestral

form. Since then a beautifully preserved, completely intact and undistorted double-rooted specimen, P_3, of *P. crassidens* has turned up. The *Telanthropus* root is more advanced, from the point of view of this evolutionary series, than any of the known australopithecine specimens but is not as advanced as the characteristic modern euhominid form. Roots not unlike the *Telanthropus* form are occasionally found among modern euhominids.

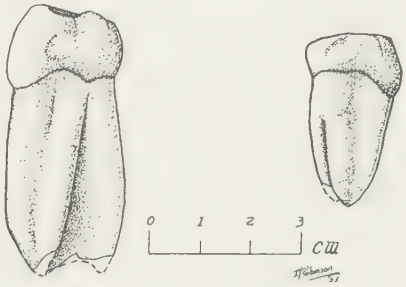

Fig. 12 Comparison of a right P_3 of *P. crassidens* with the left P_3 of *Telanthropus.*

The buccal faces of the molar crowns of *Telanthropus* differ from those of *P. crassidens.* In the latter the mesiobuccal groove is deeply incised and terminates in a pit approximately halfway down the buccal face of the crown. This pit has a well developed outer border, usually in the form of a tubercle. In no case is there a perceptible continuation of the groove below the pit and tubercle. By the time the crown is worn down so that the dentin is showing in the positions of the cusps the groove, pit and tubercle have been obliterated. In *Telanthropus* the mesiobuccal and distobuccal grooves continue almost to the cervical line, becoming less distinct as they pass down to the crown. There is no pit or tubercle associated with any of the distobuccal grooves nor with the mesiobuccal grooves in either M_3. The mesiobuccal grooves of the only M_1 and of both specimens of M_2 do have a very small pit well down the groove, which, however, passes on down the crown past the tiny pit. In no case is the slightest

sign of a tubercle present. In M_1 where the crown is worn down so that all 5 cusps have dentin exposed, the tiny pit in the mesiobuccal groove is well below the occlusal margin and both buccal grooves continue for a considerable distance below the occlusal margin. This state of affairs is very common among modern euhominids. A condition more like that of *Telanthropus* is to be found in *Plesianthropus* which, however, has the buccal face more flatly sloped. The condition found in *Telanthropus* may easily have arisen — in fact probably did — from one something like that of *P. crassidens* or *Plesianthropus*. Occasionally teeth with buccal faces almost identical with those of australopithecines are to be found among modern euhominids.

In *P. crassidens*, M_1 almost invariably has at least 6 cusps — the usual 5 as well as a tuberculum sextum in the distal wall of the posterior fovea. Over a dozen of these teeth are now known and in only one case is the tuberculum sextum rudimentary — the tooth on the opposite side of this mandible has a clearly defined 6th cusp. Unfortunately the *Telanthropus* M_1 is considerably worn but nevertheless it is fairly certain that no tuberculum sextum was present. The posterior fovea is marked by a small elongate pit close to the distal margin of the tooth. This elongate pit, however, is elongated in the same direction as the groove which separates the hypoconulid and entoconoid and enters the posterior fovea. This is the situation usual in a tooth which has no tuberculum sextum. Both specimens of M_2, on the other hand, clearly have the tuberculum sextum even though this region is nearly as strongly worn as in M_1. But in M_2 the pit is appreciably further from the distal crown margin and is elongated at right angles to the direction of the groove. Actually the transverse elongation is not so much an elongation as the remnants of a bifurcation of the groove: the 6th cusp being situated between the two grooves thus formed. This 6th cusp was of moderate size. M_3 on either side has a large 6th cusp. Clearly, therefore, M_1 had no 6th cusp, M_2 has a moderate-sized one and M_3 a large one. It might

be said that the 6th cusp is a heterogonic structure and therefore one would not expect it on the small M_1 of *Telanthropus* even though present in the much larger homologues of *P. crassidens*. This is most unlikely because it so happens that the two teeth (in SK.25 and practically unworn) which have the largest 6th cusps are very near the lower end of the size range while one of the largest specimens of M_1 (in SK.34) has only a small 6th cusp.

All the teeth have fissures which show, at the most, only the slightest traces of secondary folding of the enamel. The third molars are almost unworn and here the smoothness of the enamel surface can be seen without having to be deduced from the nature of the fissures. In *P. crassidens* moderate wrinkling of the enamel surface of the premolars and molars is common — especially on M_2 and M_3. In this form there is a distinct tendency, in both upper and lower third molars, to complication of the fissure pattern and multiplication of cusps in the talonid region. None of these features are present in *Telanthropus*. In M_1 and M_2 the fissure pattern is of a typical "dryopithecus" type while that of M_3 is slightly modified.

The *Telanthropus* mandible differs in so many respects from those of *P. crassidens*, without any intermediate specimens, that these two forms could not have been members of the same population even though they lived simultaneously in the same area.

THE RADIUS

The proximal end of a radius was found closely associated with the type mandible and P_3 of *Telanthropus*. No other bone was found in the immediate vicinity. The structure of the fragment is consistent with it belonging to the same form. The bone will not be described in detail as the features are those of modern euhominids. The maximum length of the fragment is 47 mm. The only feature which may distinguish it from the modern euhominid homologue is that the distinction between head and neck is not quite so sharp as that common in the modern specimens. The *Telanthropus* speci-

men may, however, be matched among modern euhominid specimens. In size this specimen is a little smaller than the average for the Bantu but is perhaps a little larger than the average for the Bushman.

THE MANDIBULAR FRAGMENT

The mandibular fragment has been described (Broom and Robinson, '50, '52). For the sake of convenience this fragment (SK.45) will be referred to as *Telanthropus* II, the type

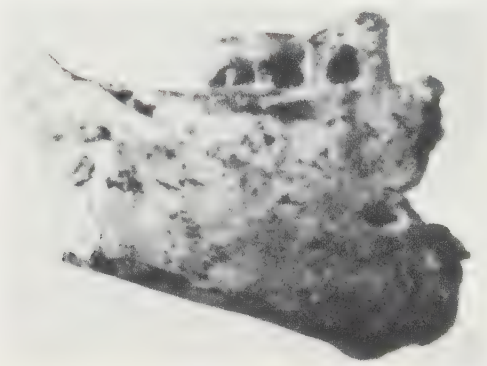

Fig. 13 Lateral view of the *Telanthropus* II mandibular fragment. Approximately natural size.

mandible (SK.15) being *Telanthropus* I. The fragment is small; on the alveolar border it reaches from immediately anterior to M_1 to just behind the retromolar triangle, while along the ventral margin it reaches from just back of the symphysis to a point immediately below the retromolar triangle. M_1 and M_2 are present: M_1 is very badly worn down and the buccal margin of the crown is worn completely away while M_2 is considerably worn with dentin exposed in the position of the protoconoid.

What remains of the mandible is less massive than that of *Telanthropus* I, but the height of the body is comparable with that of the latter. For example the maximum thickness of the body, opposite M_3, is 16 mm whereas that of *Telan-*

thropus I is 23 mm. On the other hand the minimum height of the body is the same in both, 25 mm. The greatest height of the body in *Telanthropus* I is 31 mm (between P_3 and P_4) while that of *Telanthropus* II is 36.5 mm, measured between P_4 and M_1. However at this point on the ventral margin of the latter specimen a small bony tubercle or protuberance is present. The edge of this protuberance is quite sharp and is slightly roughened as though muscle fibers originated from it and in all probability is the raised posterior portion of the digastric fossa. A Bush mandible in the collections of this department has a rather similar protuberance on either side marking the posterior extremity of the digastric fossa. The ventral body margin in *Telanthropus* I is damaged in this position on either side.

The single mental foramen is situated below the M_1–P_4 interproximal space halfway between the alveolar and ventral margins. On the medial surface of the body the mylohyoid line is clearly visible as well as the submandibular and sublingual fossae.

In size and structure the portion of body preserved in this specimen is remarkably similar to the general run of modern euhominid mandibles. It appears to be more like the latter than are either the *Pithecanthropus* B or the *Sinanthropus* mandibles.

The teeth are unfortunately fairly badly worn and nothing can be said regarding cusp number and arrangement. The first molar has the buccal portion of the crown missing but approximate dimensions can be ascertained. The buccal portions of the roots are present and intact so that a good idea of the crown breadth is possible. Allowing generously for the greater width of the crown than the roots near the cervical line, the diameter is unlikely to have exceeded 11.5 mm. The length, allowing for wear on the mesial and distal faces, is 11.8 mm, i.e. very slightly smaller than that of *Telanthropus* I. M_2 has the length and breadth, respectively, of 13.3 mm and 12.3 mm, allowing for wear. It will be seen that both teeth agree very well in size with those of *Telan-*

thropus I, both being only slightly smaller. Broom (in Broom and Robinson, '52) gives larger dimensions for M_1 but these are surely exaggerated. The width of 13 mm would produce a very exaggerated overhang of the buccal crown face. This mandible thus provides striking confirmation of the big difference in tooth size between this form and *P. crassidens*.

There is, moreover, a further interesting point about this specimen. M_3 is missing but the socket is well preserved.

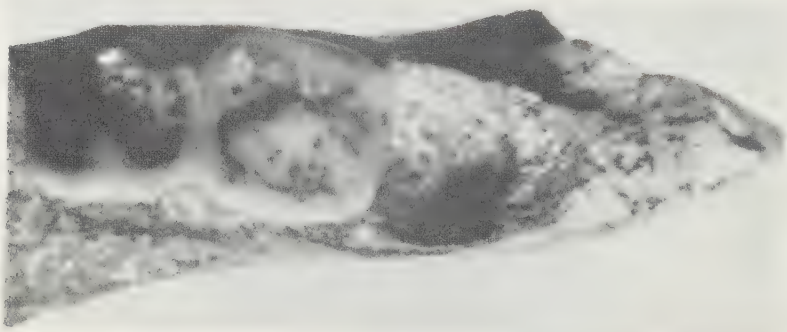

Fig. 14 Occlusal view of *Telanthropus* II showing small socket for M_3, space for only a single, fused root and the retromolar triangle. Approximately × 2.

This socket was filled with matrix and gave the impression of being long and hence of having housed a large tooth. On clearing this socket out with acetic acid recently this conclusion was seen to be wrong. A good deal of what had appeared to be socket is actually the slightly depressed retromolar triangle. The tooth could not have exceeded 10.5 mm — and probably was only about 9.8 mm — in length. The width of the alveolar part of the body across this socket is a little narrower than across the second molar and equal to the width opposite the middle of the first molar. Consequently M_3 was possibly no wider than M_1 — it certainly seems very likely that it was a little narrower than M_2. However whatever the exact dimensions of this tooth were, it is clear that M_3 was appreciably reduced in size. This is

confirmed by the fact that the roots were very reduced and directed sharply backward. Judging by the socket there appears to have been only a single, fairly small root. These considerations suggest that the tendency for reduction of M_3 which is apparent in *Telanthropus* I was more advanced in this mandible. The latter certainly could not have housed a tooth the size of M_3 of *Telanthropus* I, which also has well developed double roots.

This specimen is important in showing that the *Telanthropus* I specimen is not aberrant. In the greater slenderness of the corpus mandibulae and the reduced M_3 it is even more euhominid than *Telanthropus* I.

DISCUSSION

Before proceeding with the discussion the author wishes to draw specific attention to some of the terms used. Heberer has suggested the use of the subfamily names Praehomininae and Euhomininae to distinguish the australopithecines and the "true men" (from *Pithecanthropus* up), respectively. The subfamily name Australopithecinae was used by Gregory and Hellman ('39) at an earlier date to cover more or less the same field as Heberer's Praehomininae. It seems advisable, therefore, to adhere to normal nomenclatural procedure and use Australopithecinae as the subfamily name. Praehomininae has much to recommend it and is therefore retained by the author, not as the latinized subfamily name but as a descriptive term, prehominids, which is equivalent to the term Australopithecinae. Simpson has done the same in retaining eohippus as a vernacular equivalent of *Hyracotherium*. Euhomininae — and in the vernacular, euhominids — is used for the organisms having the grade of organization immediately above that of the prehominids. This latter usage coincides with a common scientific usage of the somewhat imprecise term "man." These two subfamilies, the Australopithecinae and the Euhomininae together constitute the family Hominidae. According to the very sensible nomenclatural principles for suprageneric categories put forward

by Simpson ('45) the above classification is not strictly correct but should be as follows: Family: Hominidae; Subfamilies: Homininae and Australopithecinae. This would remove entirely what nomenclatural basis there is for the terms prehominid and euhominid — which are very useful indeed in discussions. As the term Euhomininae does actually involve the name of the type genus, is already in the literature and this usage does in any case come very close to Simpson's unofficial rules, it seems preferable to retain it.

The geological evidence, as discussed earlier in this paper, is unanimous in pointing to contemporaneity of all specimens in the australopithecine-bearing breccia of the Swartkrans site. Specimens of different epochs are not intermingled or in adjacent pockets. *P. crassidens* specimens were recovered from above, below and the same level as the *Telanthropus* material. The latter consequently either belonged to the same local population as *P. crassidens* or are representatives of a different type of creature occupying the same territory for at least part of the time during which it was occupied by *P. crassidens.*

The first essential is therefore to determine whether these specimens could have belonged to the same population as those of *P. crassidens.* Statistical analysis shows that the odds are overwhelmingly against M_1 belonging to a member of the *P. crassidens* population, while the differences between M_2 and M_3 of the latter and of *Telanthropus* I are on the borderline of significance. The teeth of *Telanthropus* II, being a little smaller than even the *Telanthropus* I homologues, greatly strengthen this conclusion. The much reduced M_3 of *Telanthropus* II is completely unknown in any australopithecine. These two mandibles are appreciably smaller than those of *P. crassidens,* especially in respect of ramus height. *Telanthropus* II unfortunately has no ramus but clearly that of the type mandible would fit it much more nearly than would any of *P. crassidens,* which vary from a little more than one and a half times to nearly twice the height of that of *Telanthropus* I. The ascending ramus of *Telanthropus* I

differs in antero-posterior measurements at the height of the tooth row only slightly from that of *P. crassidens* but the height is much greater in the latter. In *Telanthropus* I the bicondylar width is greater than the mandibular length, measured in the sagittal plane, while the reverse is the case in *P. crassidens.*

These differences in size and shape make it quite clear that the two *Telanthropus* mandibles could not belong to the same local population as the *P. crassidens* specimens. This fact is underlined by the many morphological differences such as the nature of the mandibular foramen and mylohyoid groove, lack of a tuberculum sextum on M_1 of *Telanthropus* I, the differences in the nature of the buccal grooves of the molars, the reduced root of P_3 in *Telanthropus* I, the fused roots of M_3 in *Telanthropus* II, the simple and uncrenulated molars of *Telanthropus* I and so on.

In most ascertainable features the *Telanthropus* I and II mandibles are very similar. What remains of the buccal grooves on the M_2 of *Telanthropus* II show that they are of the *Telanthropus* I type. In size both the teeth and mandible are very similar in the two specimens except for the greater slenderness of *Telanthropus* II. A similar degree of variation is to be seen in the *P. crassidens* material and among that of modern euhominids. In *Telanthropus* II the mental foramen is situated a little further back than in the type mandible but this foramen is variable in position. The protuberance on the ventral margin below this foramen in *Telanthropus* II may or may not have been present on the type mandible but in any case it is probably not a constant character of this genus. The differences between these specimens are of the sort which one would expect between specimens of the same species and in most important features both differ to a similar extent from *P. crassidens.* The maxillary fragment *(Telanthropus* III), as has been demonstrated, differs markedly in a number of features from the homologous parts of the *P. crassidens* specimens. On the other hand its features are such as could be expected to occur in

a creature having a mandible like the *Telanthropus* I specimen. As all three *Telanthropus* specimens undoubtedly differ from *P. crassidens* and all approach the early euhominids more nearly, in structure, than does *P. crassidens,* it is logical to suppose that all three belong to the same form. There are no facts, to my knowledge, which argue against associating these three specimens. Taking everything into consideration there appears to be only one possible conclusion and that is that two hominids occur at Swartkrans: *P. crassidens* and *Telanthropus.* Teeth or jaws of one type may readily be differentiated from those of the other. Whether postcranial remains could be separated with equal facility is not easy to say. Some may be inclined to revert to the argument that the innominate bones which have been attributed to the australopithecines belong to a *Telanthropus*-like creature. If innominates were known only from Swartkrans this might have been the case but no *Telanthropus*-like creatures have been found at Sterkfontein or Makapan. The Swartkrans innominate has the same characters as those from the above two sites and therefore the only reasonable conclusion is that all three innominates belong to australopithecines.

It has been suggested that sexual dimorphism is marked in *P. crassidens, Telanthropus* merely being the female. We have remains of at least 35 (probably 45–60) individuals of the former from Swartkrans and enough variation in size is present to include both males and females, if sexual dimorphism is not strongly developed. Frequency distribution graphs plotting canine size show that there is a small amount of sexual dimorphism. Of 22 specimens of M^1 the minimum and maximum lengths and breadths, in millimeters, are respectively: 12.7–18.2 and 11.8–13.9, the smallest specimens being in the smallest jaws and vice versa. It is clear that two ill-defined size groups are represented in the material of *P. crassidens* but sexual dimorphism is not sufficient to allow a clear-cut separation of the sexes. Where sexual dimorphism is present in the higher primates the resulting differences are ones of size, not structure. The differences between *Tel-*

anthropus and *P. crassidens* involve size, proportion and structure.

There is still another point which bears on this matter. The resemblances between *Telanthropus* and the australopithecines are not all between *Telanthropus* and *P. crassidens*. One of the most striking features of the former type is the pronouncedly euhominid floor of the anterior part of the nasal cavity. None of the known australopithecines have this structure but the one that nearest approaches the *Telanthropus* condition is *Plesianthropus* — which also has a palate rather more similar to *Telanthropus* than that of *P. crassidens*. On the other hand *Plesianthropus* has a two-rooted P^3 while *P. crassidens* and *Telanthropus* have a three-rooted one.

These facts make it clear that the hypothesis of extreme sexual dimorphism is most unlikely and need not be seriously entertained.

The next step is to determine the nature of *Telanthropus* and its relationship to *P. crassidens* and the other australopithecines. It has been shown that it cannot be *P. crassidens* but it might nevertheless be one of the other known forms or a hitherto unknown australopithecine.

Plesianthropus has slightly smaller molars than is usual in *P. crassidens*, the mandibular foramen is more nearly like that of *Telanthropus* than is that of *P. crassidens* and the palate is more vaulted than is that of the latter form. In these features there is consequently a nearer approach to *Telanthropus* than in the case of *P. crassidens*. Nevertheless the teeth of the latter are more like those of *Telanthropus* in most features, although *Plesianthropus* also has buccal grooves which pass a long way down the crown and do not usually have a well defined pit. But *Telanthropus* certainly did not have the robust canines of *Plesianthropus* and the lower nasal region, especially, differs markedly from the condition found in the latter form. Although, as already mentioned, in this feature *Plesianthropus* is a little more like *Telanthropus* than is *P. crassidens*, in general the main dif-

ferences of size and structure between *Telanthropus* and *P. crassidens* are differences between an early euhominid and an australopithecine. The differences of lower tooth size, mandible size and shape and the nasal region of the snout between *Telanthropus* and *P. crassidens* apply in more or less equal measure to the other australopithecines where the corresponding parts are known. In these same features, on the other hand, *Telanthropus* approaches the early euhominids. For example the mandible size can be easily matched or exceeded among early or even modern euhominids. The slightly reduced lower third molar of *Telanthropus* I is not present even in the *Pithecanthropus* B mandible. The much reduced M_3 of *Telanthropus* II is reduced to a similar degree to that of *Sinanthropus*. The size of both specimens of M_1 (as given by the module) is exceeded by that of the *Pithecanthropus* B mandible as well as the average values for *Sinanthropus* and for the modern Australian aboriginal. The structure of the floor of the nasal cavity and the lower margin of the pyriform aperture is very like that seen in the *Pithecanthropus* specimen, but the anterior nasal spine is smaller. Spines of this same size and shape can be seen in some subfossil Bush skulls — in fact in some of the latter the nature of this general region is very similar to that in the *Telanthropus* III specimen. The distance from the anterior nasal spine to the alveolar point is greater in the latter specimen than is usual in euhominids, but it is only slightly greater than the corresponding distance in the *Pithecanthropus* IV specimen and is exceeded by that of Rhodesian man. This length, however, is also very similar to that usual in *P. crassidens*. The sections in figure 6 show clearly the differences in structure between the australopithecines and *Telanthropus* III and the similarity between the latter and modern euhominids.

The logical conclusion from these facts is that *Telanthropus* represents a distinct advance over the known australopithecines in the direction of the euhominids. It nevertheless has australopithecine affinities: for example the three-rooted

P^3, the long, bony upper lip, the wide retromolar fossa, the few slight remaining traces of buccal pits and protoconidal cingula, the anteriorly situated lingual cusp, expanded talonid and Tome's root form of P_3, the shape of the symphyseal section having the greatest thickness just above the genioglossal fossa, the relatively great antero-posterior width of the ascending ramus, etc. Most of these features may be found in some measure among euhominids — even modern euhominids. However as these features are more strongly developed among the australopithecines and as *Telanthropus* is probably older than any other known euhominid and actually lived in the australopithecine era it is reasonable to suppose that the latter were the source of these features in *Telanthropus*. The present evidence seems to allow of no other conclusion than that *Telanthropus* represents a stage between that of the australopithecines and the known euhominids. The similarities between *Telanthropus* on the one hand and either of the other groups on the other seem too detailed and too numerous to allow of any other conclusion — without adopting a complicated hypothesis where a simpler one will fit all the known facts.

The known characters of *Telanthropus* may readily be derived from the corresponding australopithecine condition. In some cases the *Telanthropus* characters fit beautifully into a series starting with the australopithecine condition and ending with that of modern euhominids. For example the common condition of the root of P_3 in the australopithecines is that of Tome's root form where there is partial fusion between an anterior and a posterior root. The plane of fusion usually runs from the mesiolingual to the distobuccal angle and usually no sign of separation remains on the distobuccal angle. There is always a large cleft on the lingual or mesiolingual face of the root. In one case in *P. crassidens* a groove is still present on the distobuccal face and in one other specimen the two roots are separate for most of their length. Clearly most of the australopithecine individuals had Tome's root form and none have yet been found which had advanced

further than the early stages of Tome's root form. A few still retained earlier stages of the fusion process. *Telanthropus* (the only P_3 now known) also has Tome's root form but a more advanced stage: the root is reduced in size, the cleft is small and does not nearly reach the cervical line. In *Sinanthropus* some roots have a still later stage of Tome's root form (the cleft is now little more than a groove) and some apparently have no groove at all. In modern man approximately 80% of individuals have a completely fused root with no grooves, the majority of the remainder having a slight mesiolingual groove.

Telanthropus is also intermediate between the australopithecines and modern euhominids in connection with the reduction of M_2 and M_3. The australopithecines normally have the molars in the following size order: $M_1 < M_2 < M_3$ but in *P. crassidens* slight traces are present of a reduction process affecting M_3. The *Pithecanthropus* B mandible has the same size order as the australopithecines but *Telanthropus* and *Sinanthropus* have the following order $M_1 < M_2 > M_3$. M_2 is therefore the largest tooth. In *Sinanthropus* M_3 is smaller than M_1 which is not the case in *Telanthropus* but this is probably an expression of the fact that M_1 is relatively small in the latter form. In the Australian aboriginal $M_1 = M_2 > M_3$ while in the South African Bantu $M_1 = M_3 > M_2$ though all the molars are almost identical in size. In American Whites the condition is just the reverse of that found in the prehominids: $M_1 > M_2 > M_3$. In all the modern euhominids, therefore, M_3 is as small as, or smaller than, M_1 — a condition not observed in the prehominids. On the other hand processes are afoot in the prehominid group in connection with tooth size which suggest that the $M_1 > M_2 > M_3$ condition could easily have resulted (Robinson, '52a). In all cases, except that of *Pithecanthropus* B, the above reasoning is based on average figures. The situation in *Pithecanthropus* will only be clarified by the discovery of additional material. The above facts show clearly that the reduction has not been achieved uniformly. The reduction process has been slowed

down or speeded up relative to the other teeth in different patterns in one group as compared to another. This is to be expected where a population is large, widely distributed and broken up into isolated or semi-isolated breeding units. The deeper palate and lesser degree of maxillary prognathism in *Telanthropus* as compared to the australopithecines are further indications of the transitional character of the former between the prehominid and euhominid groups. Another similar character is the reduced size of the roots in *Telanthropus*. In *P. crassidens* the crowns of the anterior teeth are reduced but the root size still remains as evidence of their originally larger size. The canines, especially, show this clearly. Although the crowns of both upper and lower canines are within the modern euhominid size range the roots are relatively large. In *Telanthropus* we have no canines but judging from the spacing of the sockets and the dimensions of the socket at the alveolar border, there can have been only slight differences, if any, in the crown size of the lower canine in this form and in *P. crassidens*. But the size of the root must have been distinctly smaller in *Telanthropus*. Judging from the socket size and spacing in the *Telanthropus* I mandible and the fact that the mandibular incisors and canines of *P. crassidens* had already been reduced to the size usual in modern man, it is unlikely that there was any appreciable size difference between these teeth in the two groups. Yet the postcanine teeth of *Telanthropus* have not only been reduced as a whole, but differential reduction has also occurred: in M_3 for example. *Telanthropus* therefore almost certainly did not have the big difference in size between the anterior teeth and the postcanine ones which is so conspicuous a feature of *P. crassidens*. The *Telanthropus* condition is a logical development of the *P. crassidens* condition and is foreshadowed in the reduction process already at work in the latter, as was suggested by the author in an earlier paper (Robinson, '52a).

It has been suggested to the author, in private discussion, that *Telanthropus* may merely be a macromutation from *P.*

crassidens. The argument that *Telanthropus* is different from *P. crassidens* is in no way affected by such a supposition. If the former had arisen from the latter by a saltation it would still be a different creature with a distinct genotype and evolving in a slightly different direction. However the facts set forth here do not seem to me to be consistent with such a viewpoint. There seems clear enough evidence that *Telanthropus, P. crassidens* and *Plesianthropus* represent three independent lines. Furthermore, on general paleontological and genetical grounds it seems that the tachytelic origin, by continuous rapid change, is a much more probable means of origin of a new group than saltation.

Another objection which has been raised is that *Telanthropus* could not have arisen from *P. crassidens* while occupying the same territory as the latter. This could occur, of course, if the origin was by saltation but the opinion has already been expressed that this is improbable. However the author does not wish to imply that *Telanthropus* arose directly from *P. crassidens* or, if this actually should turn out to be the case that it did so in the Swartkrans area. Two closely related forms are commonly found occupying the same territory and the obvious conclusion is that the area of origin of at least one of them was somewhere else.

The question which now arises is that of the correct classification of *Telanthropus.*

In a paper published in a previous issue of this journal, the author has attempted to show that the South African australopithecines, the so-called "*Meganthropus*" africanus from East Africa, *Meganthropus palaeojavanicus* and possibly some other specimens from the East, comprise a well defined group of creatures, the prehominids, which was spread over the greater part of the Old World in Pliocene and early Pleistocene times. The majority of these forms probably became extinct without changing their essential nature. That is, most of them were still prehominids when they became extinct. There is also a fairly clearly defined group, the

euhominids, which includes the considerable number of specimens of "true men" from *Pithecanthropus* up.

From a purely theoretical point of view the prehominids appear to be an ideal ancestral group for the euhominids because in it so many euhominid characters are actually or very nearly developed. From this point of view the prehominids are certainly far more suitable than any other known group. With the additional *Telanthropus* material it is quite clear that this form has a mixture of prehominid and euhominid characters — a fact which immeasurably strengthens the conclusion that the former group is ancestral to the latter. The fact that *P. crassidens* and *Telanthropus* were coeval and that some of the australopithecines, such as *Meganthropus*, were fairly certainly more recent in no way invalidates such a conclusion. The prehominids were clearly a moderately diversified group which must have been in existence long before the period from which have come the known forms. There has been a tendency to regard the australopithecines as a variable group inhabiting Southern Africa, but this cannot have been the case. Specimens are known also from East Africa, Java and China, and consequently this group must have been spread over the greater part of the Old World in the late Pliocene and early Pleistocene. The probability is therefore greater that they were in fact a diversified group of long standing at the time the known specimens lived. As previously mentioned the material from Swartkrans represents at least 35 individuals and consequently some idea may be gained of the degree of variation. Contrary to the opinion which appears to be generally held, the variation is not great. There is, in fact, very little variation present. This is also true of the smaller Sterkfontein collection. On the other hand the differences between the above two collections are marked. In other words the inter-site variability in this instance is much greater than the intra-site variability. The available evidence indicates that *Plesianthropus* is older than *P. crassidens*, yet in some features the former is more advanced. The evolutionary tend-

encies in the two forms do not appear to be in exactly the same direction. In passing it may be noted that *Plesianthropus* is most probably a synonym of *Australopithecus* which would then include the specimens from Taungs, Sterkfontein and Makapan. But the specimens from Swartkrans and Kromdraai differ quite markedly from the others in structure and evolutionary tendencies and separate generic status seems correct in this case. *Meganthropus* is in many ways, as far as it is known, very similar to *P. crassidens* although the region in which it lived is so far removed from that of the latter. All these facts seem to suggest a group of long standing and not a young, very variable group.

The South African forms were not all evolving along the same lines as is clearly demonstrated by the many differences between *Pleisanthropus* and *P. crassidens*. One of the lines in this group (and perhaps more than one; at present we do not know) evolved more rapidly than the others and changed from prehominid to euhominid status while the other slower-rate lines were diversifying and adapting themselves but remaining prehominid in structure. This sort of phenomenon is quite common in vertebrate history. *Telanthropus* was clearly a faster-rate line — presumably falling into the tachytelic category of Simpson ('44).

In connection with the taxonomic status of *Telanthropus* we first have to resolve the conundrum: When is man a man? The obvious answer is: When he is no longer a prehominid! That is the crux of the whole problem — what criterion can be used to mark the point at which a prehominid is sufficiently advanced to warrant inclusion in the Euhomininae?

To those who, like Goldschmidt and Schindewolf, believe in saltations, there is presumably no problem because to them the change is continuous — the transition is instantaneous. However to those, like Darwin and Simpson, who feel that the transition from one structural stage to the next is a continuous process of change without a clear gap at any point, there is a very definite problem. The perennial prob-

lem of the paleontologist — having to work with fragmentary remains of only the skeletal system — further complicates the issue.

Being an adherent of the idea of evolution by continuous change, the author feels that there cannot be any real answer to the question posed above. The transition from prehominid to euhominid must have been gradual, although it was probably achieved at a relatively rapid rate compared to the periods preceding and succeeding the transition. The transition was probably not simultaneous for various organs. It seems that from the neck down the prehominids were essentially euhominid — for instance it appears to be quite clear that they were erect walking: that the essential problems of the euhominid mode of locomotion had already been solved. The basic change from the prehominid level to that of the euhominid appears to be most directly concerned with the head, i.e. the development of a relatively large brain with the consequent skull changes. The chief distinguishing feature of "man" is his intelligence. The author does not wish to become involved here in the morass of argument regarding the nature of intelligence, its relation to the brain, the concept of mind and so forth. It seems to me that the statement that man is the most intelligent animal conveys something which is real and about which there can be no argument. This superior intelligence and capacity for reasoning has enabled man to acquire the large degree of control over his environment which is so conspicuous a difference between him and other animals. This faculty is as much a character of euhominids as are their upright posture and small canine teeth.

Attempts have been made to classify euhominids according to brain size. For example Keith ('48, p. 206) says, "I would say that any group of the great Primates which has attained a *mean brain volume* of 750 cc. and over should no longer be regarded as anthropoid, but as human." In this statement "anthropoid" is presumably synonymous with "pongid." Keith therefore regards the prehominids as pongids — as

does Simpson ('45). Whatever the origin of the prehominids may turn out to be, they certainly cannot legitimately be classified in the same family as the living great apes. If those who think that the prehominids diverge from a pongid stock are right then far enough in the past there must have been ancestral forms of the australopithecines which could legitimately be classified as pongids. In the author's opinion no portion of the ancestral line of the prehominids can rightly be so classified.

Modifying Keith's statement to the effect that an average cranial capacity of 750 cm^3 and above should distinguish euhominids from prehominids still does not make it altogether satisfactory. If a group is very variable a mean value is not very satisfactory and we know that endocranial capacity is a character subject to wide fluctuation in euhominids, varying from slightly above Keith's "rubicon" to three times that value. Furthermore a mean value is not a good character to use in connection with fossil material where one often has only a few specimens which are very fragmentary. Comparatively little is known about the relation of brain size to intelligence, except in very general terms, and it is quite conceivable that a prehominid brain of 600 cm^3 volume may represent a very different level of intelligence to that of a pongid brain of the same size. There is also evidence which suggests that the brain volume of *P. crassidens* was about 750–800 cm^3 — which would make it an euhominid according to the above criterion. In the author's opinion the possibility of this being so is very slight — *P. crassidens* is a prehominid.

Le Gros Clark ('49) and Oakley ('51) have suggested that a more suitable criterion is an objective indication of a certain level of intelligence, such as the manufacture of stone implements. This is manifestly a more suitable and practical solution to the problem, but it is only a partial solution.

Once stone implements occur there can be no doubt that a true euhominid is being dealt with. But what of the early crude implements? Here again there is a transition from the roughly broken article to the artifact showing unmistakable

evidence of human handiwork. Artifacts from the early stages of this transition could be mistaken for naturally broken stones and vice versa. This is not the only objection which can be raised against this criterion. All experience in connection with the initiation of something entirely new on the part of man suggests that in the early stages progress is extremely slow. Is it not therefore reasonable to suppose that the euhominid stage was in fact reached an appreciable time before the manufacture of stone implements was hit upon and developed into a recognizable cultural attribute of man? The difference between the technological achievements of the ancient Egyptians or Greeks and those of our present society is surely not attributable to a much higher level of intelligence on our part but is rather a matter of realizing potentialities. It seems likely that the mental and physical equipment which could allow a creature to manufacture tools would have been present for a considerable time before such manufacture actually became established. In that case there is no reason why this pre-artifact stage should be considered any less euhominid than the early artifact stage. In the author's opinion, therefore, the systematic manufacture of artifacts marks a stage distinctly later than that at which euhominid status had been reached. Unfortunately there does not seem to be a better criterion than that of the manufacture of artifacts. This is therefore very useful where it is positive, i.e. when artifacts occur euhominids were in existence, but the absence of artifacts does not *ipso facto* mean that the creature concerned was not an euhominid.

All of this makes it difficult to assess the exact status of *Telanthropus*. No artifacts have been found associated with this form nor with any of the australopithecines. Although only fragmentary remains of *Telanthropus* are known, these are among the most illuminating and instructive parts of the skeleton. In view of the fact that this form is so similar to the early euhominids, and in at least one feature (reduction of M_3) was more advanced than *Pithecanthropus robustus*, it seems clear that it was either near the end of the

transitional phase or had already reached an essentially euhominid status.

Telanthropus was not necessarily directly ancestral to modern man but may have been part of the early stages of a radiation once the euhominid organization had been achieved. It is likely that the prehominid-euhominid gap was bridged only once and *Telanthropus* seems to be closer to the central part of this evolutionary stream than the other known early euhominids, especially if prehominid characters are taken into account as well. For example the diastema of *Pithecanthropus* and the excessive wrinkling of the enamel of *Sinanthropus* are not characteristic of the prehominids or of *Telanthropus*. It is also most unlikely that *Telanthropus* had large canines such as those possessed by the two eastern forms. As *Telanthropus* and at least some of the prehominids already had more nearly modern forms of the above features, it seems quite probable that *Pithecanthropus* and *Sinanthropus* represent an early development away from the central stream — as Neanderthal man represents a later swing away. Only additional material will enable one to decide whether this interpretation is correct. It seems to me that the important thing to appreciate about *Telanthropus* is that while it resembles the prehominids in some ways it also has some characters which are at present only known in euhominids. It therefore links these two groups together.

A further point of interest is the endocranial volume of *Telanthropus*. This has not been dealt with before because the only evidence bearing on this point is indirect. Nevertheless it seems to the writer that the line of reasoning involved is worth pursuing, as long as it is appreciated that the result can only be an order of magnitude and not a precise figure.

In *P. crassidens* the mandible is well known and in every case the ascending ramus is relatively high. This is, as far as the evidence goes, also true of the other prehominids. *P. crassidens* has an endocranial volume of about 750 cm^3. This cannot be directly measured but this figure may be arrived

at as follows: the Taungs child's endocranial volume is generally considered to be about 500 cm^3. More than half of the braincase and endocranial cast is present and the determination of the volume within a small percentage of error is possible. The adult volume, it is generally agreed, would probably have been about 600 cm^3. The skull of a child of *P. crassidens,* of exactly comparable dental age (i.e. the only permanent tooth erupted is M^1) is known. This is crushed but the crushing is of such a nature that the length and breadth measurements can be found with a fair degree of accuracy. Even the height may be ascertained, in a graphic reconstruction, by following (with a steel tape or similarly flexible rule) the midline, which is easily done as the sagittal suture is easily identifiable, and then fitting the steel tape onto the measured base and bending it into a curve of the australopithecine shape so that the measured length fits between the glabella and the maximum occipital point. All the bone surface, in the sagittal plane, is present but pushed out of position, hence the above procedure is not difficult. The measurements of this skull show that, while the height is much the same as that of the Taungs skull, the width and length are greater: in the length there is a difference of some 25 mm and in the breadth slightly more. As the greater part of the cranial vault in all the known australopithecines consists of thin bone of much the same thickness, differences in overall measurements reflect, almost entirely, differences of endocranial volume. From the measurements of the young *P. crassidens* skull it seems clear that it is appreciably larger than the Taungs skull. The difference in volume could not very well be less than about 100 cm^3 That is, the child *P. crassidens* must have had an endocranial volume approximately equal to the adult *Australopithecus africanus.* The endocranial volume of an adult *P. crassidens,* which had an endocranial volume of about 600 cm^3 at the time of eruption of M^1, would be about 720 cm^3. The adult skulls of this form now available show that an average capacity of about 750 cm^3 is reasonable and may even be on the conservative side.

The high ramus of the *P. crassidens* jaw reflects the fact that the glenoid fossa, and hence the base of the skull, is rather high above the level of the occlusal plane of the teeth. But the skull of this form has a very low forehead — even lower, relatively, than the smaller-brained *Plesianthropus* — and the vertex is not much above the level of the supraorbital torus.

The bicondylar width of the mandible in *P. crassidens* is approximately the same as in *Telanthropus* and modern man. But the *Telanthropus* mandible has a very much lower ascending ramus than has that of *P. crassidens*. In other words in this form the base of the skull must have been at very much the same level as the occlusal plane and considerably lower than it is in *P. crassidens*. The skull width must have been much the same in these two types because of the similarity in bicondylar width. The *Telanthropus* skull could not very well have had a lower vertex than that of *P. crassidens* as this would have produced an abnormal skull with the supraorbital torus higher than the vertex. Even assuming the heighth and width of the *Telanthropus* skull to be the same as that of *P. crassidens* the lowered cranial base must mean greater endocranial volume. Even allowing for the possibility of the vault bone of *Telanthropus* being a little thicker than that of *P. crassidens*, the difference in endocranial volume could not have been much less than 100 cm^3 as the difference in ramus heights is over 30 mm. However since one of the greatest factors in the brain enlargement would almost certainly be increased size of the cerebral hemispheres it seems more than likely that the downward movement of the skull base will have been accompanied by a slight upward expansion of the vault as well as a small amount of lateral and backward expansion. If *P. crassidens* had an average brain size of about 750 cm^3 it seems impossible that *Telanthropus* had a brain any smaller than *Pithecanthropus* — a likely figure is about 850–900 cm^3. This line of reasoning naturally contains a lot of speculation and was not included in the descriptions of the specimens because of that fact. However

there seems to be nothing inherently unreasonable in it. After all, the features of these specimens show a distinct advance over *P. crassidens* in the euhominid direction and as this change is so much bound up with increase in brain size it is logical to suppose that the changes in teeth, palate, nose and mandible will have been accompanied by at least a small increase in brain size. The above reasoning attempts to show that the slender evidence available is in harmony with such a supposition.

From all the foregoing it is manifest that while the significance of *Telanthropus* is quite clear, assigning a definite status to it is more difficult. The known anatomical features appear to be closer to those of the early euhominids than to prehominids. It would seem that this form had just about completed the transition from prehominid to euhominid and quite possibly was in the pre-implement, euhominid stage. A very interesting parallel may be drawn here. Prehominids occur in the East. The best known is *Meganthropus*. This form most nearly resembles *P. crassidens*. In the same site a very primitive euhominid, *Pithecanthropus robustus*, has been recovered. No implements were found associated with the latter. The differences between the Javanese prehominid and euhominid at Sangiran are of the same order as those between the corresponding forms at Swartkrans. In the fullness of time when, we hope, many more specimens of these are available, may it not perhaps turn out that *Meganthropus* is a *Paranthropus* and *Telanthropus* a *Pithecanthropus?* It seems possible. However this may turn out, it is certainly true that both sites contain an australopithecine as well as a more advanced form. The Javanese *Pithecanthropus* is clearly an euhominid. *Telanthropus* with its reduced M_3 and probably large brain seems to be at a comparable evolutionary stage and fortunately retains clear indications of its ancestry. In age it appears to be either early Villafranchian or late Upper Pliocene and is therefore appreciably older than *Pithecanthropus robustus*. This specimen is there-

fore of much interest and importance for the understanding of hominid phylogeny.

CONCLUSIONS

1. *Telanthropus* could not have been a member of the same population as the known *P. crassidens* specimens.

2. It has distinct australopithecine affinities but not all of these are with *P. crassidens*. In some features it more nearly resembles *Plesianthropus*.

3. Some of the *Telanthropus* characters are unknown in the available australopithecine material.

4. Precisely in these characters it is progressive and resembles the early — or even some modern — euhominids.

5. *Telanthropus* therefore links the prehominid and euhominid groups together in possessing characteristic features of both.

6. *Telanthropus* had actually, or very nearly, completed the transition from prehominid to euhominid status.

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PIGMENT CELL GROWTH. By Myron Gordon (ed.). Academic Press New York. 365 pp., 1953.—"Pigment Cell Growth," the published proceedings of the third conference on the biology of normal and atypical pigment cells, consists of 22 separate papers ranging from structural chemistry to the epidemiology of melanomas. The considerable but previously scattered information on the brown black pigment, called melanin, is thus made available in one volume, and by a distinguished group of scientists.

Approximately one-third of the pages refer directly to man, and since the basic principles of melanogenesis are similar from bananas to Bantu, all of the book relates at least indirectly to problems of anthropological interest. Hutt's article on the genetic control of pigmentation in the fowl, and the paper by Berg and Gordon on hormonal factors in pigment cell growth (in fishes) demonstrate the kind of information that it is possible to acquire.

Of the chapters pertaining to man, those on the epidemiology of melanomas are interesting because they touch on solar radiation as a co-carcinogen, and the evidence for reduced susceptibility in Negroes. Edwards' paper (on the dermal spectrophotometer) is especially noteworthy, for one suggestion he made during the Pigment Cell Conference in 1951 (on the use of dermal spectrophotometry in endocrine disorders) has since been followed up by Thorn and his group.

Most stimulating, perhaps, to those of us who have faced the limitations of conventional skin color investigations, is the paper by Alice Baker. Though her experimental animals were frogs, there is no reason why similar studies may not be profitable in man. The fact that *Rana Burnsi* is both darker than and contains more tyrosinase in its skin than *pipiens*, as Baker has shown, is an obvious and not to be neglected clue as to what one of the "factors" in the inheritance of human skin color must be. (The other factors must include dopase, and possibly an enzyme co-active in melanin oxidation.)

Though much of the book is moderately technical, "Pigment Cell Growth" is a necessary prerequisite to any intelligent understanding of the normal pigment cell.—S. M. GARN.

A FUNCTIONAL ANALYSIS OF THE FACIAL SKELETON WITH SPLIT-LINE TECHNIQUE

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FIVE FIGURES

The biological meaning of many of the characters used by anthropologists in problems of taxonomy and group history remains virtually unknown or in dispute. Recently Hooton ('46) admitted that little is known of the adaptive or non-adaptive value of most hereditary variations used in anthropological classification. This is in contrast to Hooton's ('31) earlier extensive list of characters he then regarded as non-adaptive and therefore suitable for taxonomy. Similarly, the extent to which morphology is genetically or functionally determined frequently remains undecided in problems of fossil man (Howell, '51) and modern races (Coon, Garn and Birdsell, '50). All the above authors offer stimulating hypotheses on the interpretation of form differences but give little direct demonstration of their validity. It seems clear that more techniques of analysis are greatly needed by anthropologists if the science is to progress satisfactorily.

Functional analysis of morphological traits is still in its infancy (Schaeffer, '50), but its ramifications are already clarifying many problems of anatomical form. In the facial skeleton, one promising aid to analysis is the Benninghof split-line technique. It demonstrates the orientation of the minute architecture of compact bone by staining methods. Benninghof ('25) was able to show that some areas of the skull were directionally organized in their split-line patterns, particularly in the face, while other areas, notably the skull-

cap, showed no such organization. Benninghof ('25, '27) and Seipel ('48) have given evidence that the patterns of organization are related to the mechanical forces acting on the facial skeleton.

The method has not been used extensively since its introduction. Benninghof ('25, '27) was principally concerned with its introduction and the demonstration of its relationship to cancellous bone organization and mechanical stresses in the compact bone. Henckel ('31) processed skulls of chimpanzee, baboon, *Semnopithecus*, orang and man. His descriptions are very brief, however, emphasizing the similarity of pattern among these primates. The differences are not adequately described. His generalized drawings do not indicate satisfactorily the direction and meeting-points of some of the split-line systems. Bruhnke ('29) confined his study to mammals other than primates. Seipel ('48) concerned himself chiefly with the stress systems in the face and lower jaw and their application to orthodontic problems. He outlines a scheme of trajectories of the face which are related to the force of the chewing muscles as well as the pressure from the tooth row. It is frequently not clear which direction he believes these stresses take, however, and the nature of several of his trajectorial structures is not explained.

None of these investigators gives adequate attention to the variability to be found in the split-line patterns. There has been little careful comparative work. Some areas of the face have never had their split-line patterns reported, such as the nasal surface of the maxilla and the temporal surface of the zygomatic bone. Some patterned areas have never been interpreted. Finally, none of the previous workers has been primarily interested in anthropology. There has consequently been little discussion of anthropological problems, and the relationship of the form of various regions of the facial skeleton to their split-line patterns has never been discussed and tested adequately. With these limitations to present knowledge in mind, further investigations using the split-line technique were undertaken.

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MATERIALS AND METHODS

Split-line preparations were made on the adult facial skeletons of 6 human beings and one chimpanzee. Special preparations were made on two dog and one cat specimens for a supplementary problem. Human material was in two cases commercially prepared specimens of unknown provenance and in 4 cases male dissecting room material. Dentition was good or excellent in all specimens, a maximum of one tooth being missing on any side.

The split-line technique has been described most thoroughly by Seipel ('48). It consists essentially of decalcifying the compact bone in weak acid (in this case 10% HCl) sufficiently to allow easy penetration by a sharpened teasing needle. These perpendicular punctures of the surface bone usually form short fissures rather than round holes. India ink is then introduced into the splits, usually less than ¼″ long, to clarify their direction. Seipel has shown histologically that these fissures correspond to the direction of orientation of a majority of the Haversian systems in the particular area of the puncture. The split-line technique thus samples the minute organization of compact bone.

It was found that a hypodermic needle dipped into the ink and inserted alongside the teasing needle while it was still holding the split open introduced the color satisfactorily. Excess ink at the surface was wiped away with a damp cloth. Frequent re-wetting aided puncture, distributed the color more evenly and made for easier closure of the fissures. The material was allowed to dry out when not being processed, since the bone tends to mold and deteriorate if it remains moist for long periods of time. A brief soaking in water was adequate to resoften the specimen.

In the more highly organized areas of bone it was usually possible to join the fissures together in continuous lines by

making intermediate punctures, in the same manner as Seipel ('48). This made demonstration much clearer, and gave clear indications of the meeting points of divergent systems of split-lines. Continuous patterns are apparent in figures 1

Fig. 1 Split-line preparation of face and brow region of human male. White squares of paper are on zygomatico-maxillary suture.

and 2. The meeting points of continuous systems may be particularly noted in the zygomatic region of the specimen in figure 1.

In areas where the splits gave no indication of uniformity of direction there was no attempt to join them. In the more highly organized areas the direction of the split-line patterns could not be an artifact or a creation of the investigator. On

more than one occasion preconceptions as to the direction the patterns would take were disproved by the actual orientation of the splits.

Seipel ('48) found that the split-line pattern in two regions of the mandible was different, in some specimens, in deeper layers from what it was at the surface. Accordingly, the surface bone of two of the human specimens was whittled down and split-line preparations were made, to test the uniformity of direction of split-lines at different depths.

To help assess the extent of correspondence between bony structures of different thickness and split-line patterns sectioning was performed on one side of the face of two undecalcified specimens, and sectioning and disarticulation of bones on three decalcified specimens. Measurements and observations not otherwise possible could thus be taken. From this material an attempt was also made to evaluate the correspondence between split-line patterns and observable patterns of trabecular bone in the face.

The procedures outlined above give the most extensive picture to date of the variability in split-line patterns of the human face, and allow discussion of the comparative analysis of similarities and differences of pattern between man, another primate, and other mammals. Regions of the face previously unreported, the interior surface of the frontal region, the temporal surface of the zygomatic bone, and the nasal surface of the maxilla, help greatly in clarifying the total functional picture in the split-lines of the face.

OBSERVATIONS

Unless otherwise stated, all subsequent descriptions refer to human specimens. Except for special preparations, figures 1 and 2 illustrate all the points made. Descriptions of the split-line patterns of separate regions of the human face are given, along with variations noted in different specimens. The situation in each corresponding region of the face of the chimpanzee specimen is described immediately after each region

in man. Preparations were not made in any region of the chimpanzee specimen other than in the external face, however.

Alveolar margin. Immediately above the tooth row in the alveolar process of the maxilla, a split-line pattern can in some specimens be observed quite clearly, running parallel to the

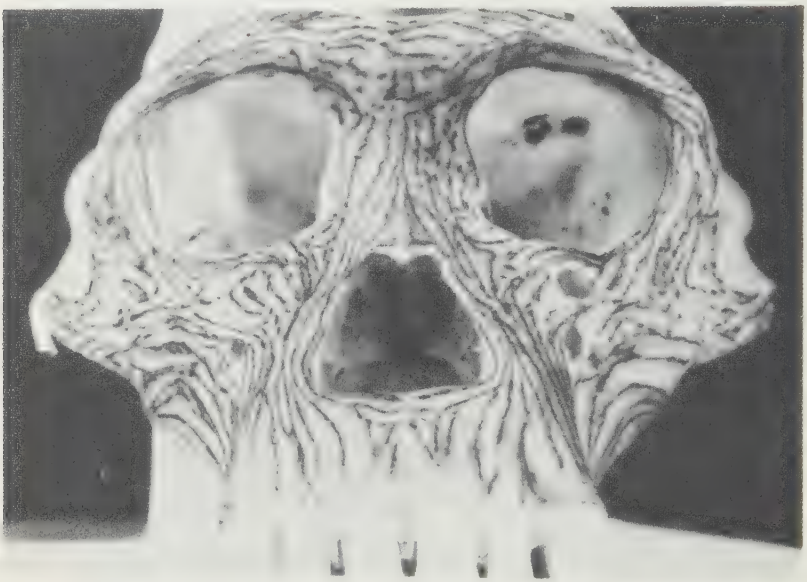

Fig. 2 Split-line preparation on face and brow region of adult male chimpanzee.

inferior border of the alveolar process. Its failure to appear in the others may be due to excess decalcification of the very thin bone. This pattern may be 3 or 4 mm in height in the molar region, where it is continuous, and where there is often a slight but continuous ridging of bone which corresponds to the split-line pattern. The ridging and the continuous lines become less well-defined or disappear above the premolar teeth. The height of the pattern becomes reduced. In the canine and incisor regions the pattern may disappear completely. Where it remains, it is found at the base of the tooth socket itself, but the pattern may be missing above the

interalveolar septa. The pattern just described is closely paralleled on the lingual side of the alveolar process, but here it courses parallel to the split-line pattern of the palate described by Seipel ('48).

The chimpanzee is an exception in that the highest extent of the pattern is found above the canine tooth rather than above the molars. No ridging is observable here.

The two specimens which did not reveal the pattern have extremely thin alveolar bone in the canine and incisor regions. In one case where a missing tooth had been followed by resorption, there was no trace of the pattern. In the above cases it was usually difficult to obtain any clear split-lines.

Alveolar process of the maxilla. Above the immediate alveolar border region, the alveolar process of the maxilla shows a generally vertically oriented split-line pattern. This may begin immediately at right angles to the lines running parallel to the inferior alveolar border, may begin as lines curving sharply away from the latter region (as seen in fig. 1), or may begin in some parts of the face only at a height of two or more centimeters above the alveolar border. In those specimens showing such a gap the vertical split-lines were less regular and well marked. These were the same specimens in which the alveolar border pattern was not detectable.

The ascending split-lines are clearest in the region of the zygomatico-alveolar crest. They are also usually well marked above the canine tooth, coursing beside the lateral border of the piriform aperture. Between these two areas there is more tendency toward irregularity of the split-lines. This is not observable in the chimpanzee.

From the incisor teeth the split-lines ascend toward the nasal aperture, veering somewhat laterally as they approach its inferior border to become part of the system of ascending lines originating from the canine tooth area. Even the most medial lines lead into this system in those skulls in which the border of the nasal opening remains sharply defined throughout. In the two specimens whose nasal floor is continuous with the surface bone the ascending lines enter

the nasal cavity, though there is some lateral divergence. Although the nasal situation in the chimpanzee resembles the last-named pattern, the ascending split-lines never reach the inferior border of the nasal aperture. Immediately below the inferior margin of the nares the lines closely parallel the border and meet at the midline.

The ascending split-lines above the canine and incisor teeth do not extend very far. The more medial ones parallel the superior margin of the nares and end on the inferior portion of the nasal bone. They may lose their organization before extending this far, as is the case with the specimen shown in figure 1. This individual had suffered a fracture of the lower part of the nasal bones, however. Those ascending split-lines which begin more laterally above the canine tooth are interrupted by the system of split-lines which roughly parallels the inferior orbital margin.

The ascending split-lines in the region of the zygomatico-alveolar crest are also interrupted completely by systems of split-lines coursing at approximate right angles in the zygomatic region. In some specimens, as in figure 1, some of the ascending lines may abruptly change course, turning laterally and downward to conform to this predominating pattern.

Lower orbital margin. Thus all ascending split-line patterns in the alveolar process of the maxilla are completely interrupted by generally continuous lines beginning in the frontal process of the maxilla, traveling along the infraorbital region, and continuing downward, laterally and backward to the region of origin of the anterior portion of the external part of the masseter muscle. In figure 1, the white squares of paper mark the zygomatico-maxillary suture, illustrating how the continuous organization of split-lines is independent of the bones in which the lines course. Continuous split-lines cut straight across the suture line immediately below the orbit, and course roughly parallel to the suture on both maxillary and zygomatic sides in the malar region. The lower limit of this organization pattern is coincident with the lower border of the tendinous origin of the masseter mus-

cle. The muscle boundary is below the suture line on the zygomatic process of the maxilla (Sicher, '49).

The continuous internal architecture revealed by the split-line pattern just described has a general structural correspondence in the gross form of the bone. The lower orbital margin is usually sufficiently thickened to form what Weinmann and Sicher ('47) term the *infraorbital buttress.* The

Fig. 3 Split-line preparation on human adult, indicating intermittent continuation of split-line pattern of lateral brow region into central brow region. Infraorbital split-line pattern interrupting ascending lines in nasal region can also be observed.

more clearly defined this is as a structure, the more closely the split-lines correspond to it. The correspondence is generally greatest above the infraorbital foramen. Medial to this there may be a considerable fanning out of the split-lines, only the most closely approximated ones continuing to parallel the orbital margin. In one specimen the thickening did not continue along the orbital margin into the frontal process of the maxilla, but continued straight across to the region just above the nasal opening, the confluent split-lines forming a striking contrast to the generally vertical lines above and below it. This is shown in figure 3.

Canine fossa. Up to this point three well marked systems of split-lines have been noted in the face: (1) ascending lines above the canine tooth region, coursing alongside the narial margin; (2) ascending lines above the first molar tooth associated with the zygomatico-alveolar crest; (3) laterally directed lines running below the orbit and in the zygomatic region. The area bounded by them varies with the extent of these highly organized systems, but the infraorbital foramen usually marks its highest point. The bone is usually quite thin in this region. Here a depressed canine fossa may be observed in some specimens. The split-line pattern usually shows some degree of disorganization in this region, although one specimen has clear ascending lines throughout, in spite of a well marked fossa. Another specimen shows a disorganized split-line pattern here in spite of the absence of a canine fossa.

The chimpanzee shows some marked differences from the human situation in the split-line patterns of the face. The ascending split-lines coursing from the canine region alongside the nasal aperture do not terminate above it, but continue up to the brow ridge region. There is no general system of infraorbital split-lines continuing over into the zygomatic region and area of origin of the masseter muscle. Instead, the split-lines continually branch off laterally from the ascending pattern. At the highest level, the lines ascend into the orbit. More lateral ascending lines are either bent later-

ally into the zygomatic region or are cut off by a short pattern of lines bounding the inferior margin of the orbit. These do not continue in the zygomatic region. They are cut off by lines associated with the lateral boundary of the orbit, descending to meet the horizontal lines in the zygomatic region. Lines ascending from the molar region anterior to and in the zygomatico-alveolar crest turn back downward to stop at the lowermost point of origin of the masseter muscle. No canine fossa is observable. It should be noted that the zygomatic arch and masseter muscle are both lower in relation to the inferior margin of the orbit in the chimpanzee.

Zygomatic arch. In the human, the split-lines in the zygomatic region previously described, which are associated with the origin of the masseter muscle, become directed more and more backward as the zygomatic arch is approached, finally becoming continuous with lines which course in the direction of the axis of the zygomatic arch.

Lateral orbital region. Lateral to the orbits organized split-lines course approximately vertically, parallel to the orbital margin. These usually begin in the frontal bone, coursing through its zygomatic process and across the zygomatico-frontal suture to descend as far as the body of the zygomatic bone below the level of the inferior orbital margin. In two specimens this pattern is clearer at deeper levels than at the surface, where minor irregularities occur.

The more posterior lines turn at the level of the zygomatic arch to become continuous with the lines running in the direction of the axis of the arch. This transition does not occur in the specimen shown in figure 1, where the lines in the anterior part of the zygomatic arch parallel its inferior border rather than the superior margin. This is the only specimen discovered with this deviant pattern. More anteriorly, the descending lines paralleling the lateral border of the orbit are either cut off by the lines continuing in the zygomatic region from the infraorbital area, or die out in an area in which the split-lines become random or do not appear at all

when the decalcified bone is punctured. Close to the orbital margin the lines continue to parallel the orbital margin around its lateral inferior flexure. These lines join the infraorbital system of split-lines.

Supraorbital region. The region above the orbits is marked by considerable variability in split-line patterns. The lines previously mentioned which are continuous with the lines running lateral to the orbit in the frontosphenoidal process of the zygomatic bone are usually confined to the area Cunningham ('08) has described as the *trigonum supraorbitale* of the frontal bone. This triangular area is lateral to the supraorbital foramen. In one specimen, however, some of these lines continue, with occasional interruptions, as far as the midline, seen in figure 3. Another specimen shows only random split-lines in the trigonum on one side, though the typical pattern appears on the other side. The superciliary ridge region usually shows only random split-lines or round holes and diffuse spots where the ink entered. One specimen shows a brief, narrow area of organization along the ridge. Three specimens show a tendency to continue lines circumorbitally from the frontal process of the maxilla into the frontal. These lines are never strong or extensive, however. No relationship to frontal sinuses was observable. The sinuses ranged from absent to very extensive in the individuals processed.

In contrast to the human specimens, the chimpanzee shows very definite split-line organization in the brow region. The lines close to the orbits continuously parallel them superiorly and medially as well as laterally. The frontal sinus of this specimen is extensive, reaching approximately to the midpoint of each orbit.

Infratemporal surface of the maxilla. Posterior to the zygomatico-alveolar crest above the first molar the split-lines course vertically in the alveolar process of the maxilla. Further back on the infratemporal surface of the maxilla the bone becomes very thin, the maxillary sinus being greatly extended. In some specimens the split-line pattern becomes ran-

dom in this region, while in others the vertical orientation of the split-lines is maintained. The chimpanzee pattern is random here.

Nasal bones. Split-lines in the nasal bones run vertically along the axis of the bones until the region above the nasal opening is reached. At this point the pattern may become random, or the lines may be directed laterally, continuous

Fig. 4 Split-line preparation of maxilla and temporal surface of right zygomatic bone, viewed from behind. Molar teeth are to the right, incisors to the left. Above the incisors is the right half of the nasal opening. More anterior ascending lines from maxilla are deflected to the right along the inferior margin of the zygomatic bone. More posteriorly, lines ascending along the wall of the braincase reverse their course and descend at the back of the lateral orbital region.

with lines in the maxilla which parallel the nasal aperture. The lines in the chimpanzee are continuous with those from the maxilla.

Fig. 5 Split-line preparation on the nasal surface of the left maxilla. Left central incisor tooth is visible below right, premolars and molars to the left. Nasal conchae have been removed. Above the incisor is the outline of the nasal opening with split-lines coursing parallel to the margin. Split-lines also parallel the nasal bridge anteriorly, ascending to the frontal region. More posteriorly, split-lines are continuous from floor of nasal cavity to the frontal bone.

Interior surface of frontal region. No split-line pattern was observed in the area posterior to the frontal sinus and brow region. This appears to be part of the general inner table of compact bone of the skull. The bone is laid down in a series of thin, extensive layers which can be readily teased apart in the decalcified condition. No pattern of split-lines is apparent, and the individual splits are independent

of each other in direction from layer to layer. This condition is encountered nowhere in the face region.

Temporal fossa region. Special split-line preparations were made of the region of the temporal surface of the zygomatic bone and adjacent portions of the temporal fossa in three specimens. Figure 4 illustrates the results on the zygomatic bone. The lines proceeding upward immediately behind the zygomatico-alveolar crest turn at the level of the zygomatic arch and proceed backward along the axis of the arch, paralleling those on its external surface. Those beginning farther back on the infratemporal surface of the maxilla continue upward, although they may be somewhat irregular in direction. On the internal face of the frontosphenoidal process of the zygomatic bone the lines closest to the posterior border of the orbital boundary run upward parallel to that boundary. Farther away from the boundary, on the postero-lateral surface of the orbital process of the zygomatic bone, the lines loop over toward the sphenoid bone and may begin to descend before they ever reach the sphenoid. The lines that begin farther away from the border progressively loop over it a lower level. All of these lines are continuous with those coursing in the zygomatic arch parallel to its axis. At the other end of this system of looped lines, they may continue to run downward in the sphenoid bone, but their course is irregular when they do so.

Nasal surface of the maxilla. In two specimens a special split-line preparation was made on the nasal surface of the maxilla, shown in figure 5. The nasal conchae were removed. Anteriorly the split-lines conform to the external pattern, with lines ascending parallel to the border of the narial margin and ending on the nasal bone. Anterior lines in the superior part of the maxillary frontal process descend and end at this same focal point. More posteriorly, however, the split-lines run continuously from the floor of the nasal cavity to the frontal bone. The pattern here has no interruption by lines paralleling the inferior border of the orbit, such as is seen superficially.

Deeper layers. In no part of the face region is the split-line pattern in deeper layers of compact bone significantly different from the surface pattern. This was tested both by whittling down after the split-lines had been made and by whittling away the bone on the opposite side of the face of one specimen before attempting split-line preparations. However, in regions where there is cancellous bone underlying, the split-lines do not appear at all in the transitional levels. Seipel ('48) also found this to be the case.

Skull sections. There is considerable correspondence between highly organized systems of split-lines and thickening of the bone in the face, revealed by sections of undecalcified and decalcified skulls. The infraorbital region is continuously thickened in the direction of the split-lines. The zygomatic region, zygomatic arch and lateral border of the orbit are all thickened and have definite split-line patterns. This is also true of the *canine pillar* of Weinmann and Sicher ('47), its continuous split-lines being observable on the nasal surface of the maxilla.

A strong exception is the brow region, where thickened bone is not accompanied by highly organized split-line patterns. On the other hand, well organized patterns are found in some regions in which there is very little thickening of bone. This is the case in the zygomatico-alveolar crest and the region of the maxilla bordering the superior margin of the narial opening.

In general, cancellous bone is scanty or absent in the face. It appears only in thickened bony areas, but usually makes up a minor part of the area of any cross-section of these thickenings. Trabecular organization is usually weak or absent, as Benninghof ('25) observes for most flat bones.

The dog and cat do not have a complete post-orbital bar. Instead, there are bony processes originating from the zygomatic arch, connected in the living state by a tough band of connective tissue. At these origin points the split-lines deviate from their antero-posterior courses in the frontal bone

and in the zygomatic arch to enter these processes and run in the direction taken by the fibrous band of connective tissue between them.

DISCUSSION

The meaning of the Haversian system organization revealed by the split-lines is not fully understood at present. The response of many split-line systems to mechanical stresses is probable but has not been demonstrated experimentally. The changes in split-line patterns shown by Benninghof ('27) on femurs bent by rickets, and by Seipel ('48) on a mandible which was broken and imperfectly reset, indicate such orientation. Seipel also found that the split-line pattern along the alveolus of the deciduous canine tooth of young chimpanzees became completely disorganized during the period of eruption of the permanent canine. Figure 2 shows that the pattern has become reorganized in the adult. It is thus indicated that split-line patterns here are related to the mechanical force of chewing rather than to the direction of growth of the tooth.

In a number of areas of the face well marked split-line patterns coincide with thickened bone, such as the lateral orbital and infraorbital regions. This again may indicate that the split-line patterns correspond to chewing stresses, provided thickened bone can be demonstrated to be directly related to such stresses. If structures and split-lines are functionally developed in response to stress, this may be demonstrable experimentally by operations in which stresses are reduced or eliminated on one side of the face, and others in which sections of organized bone are removed and reset at a different angle.

In contrast, the split-line technique may be useful in the indication of structural features which are independent of strongly oriented mechanical stresses. Both Benninghof ('25) and Seipel ('48) observed absence of split-line patterns in well-developed mental protuberances. The thickened bone of the skullcap was observed by Benninghof to have no definite

split-line patterns, and this study verifies his finding that there is no consistent split-line organization in the adjacent human superciliary ridge. In these cases there is either little or no mechanical stress, or the bone is so thick that its minute architecture is unaffected by stresses. In either case the thickness of the bone must result from something other than a functional response to pressures or tensions on it.

The definite split-line patterns observed in this study are interpreted as a response to pressures and tensions set up in the face by chewing. It is assumed that Haversian systems can be oriented in the direction of either tension or pressure, although Benninghof ('27) and Murray ('36) are divided on this question on theoretical grounds.

It should be possible in the future to determine instrumentally the direction of stresses in the bone of living, moving animals. Gurdjian and Lissner ('44) used an electric strain gage to record tension and pressure areas resulting from blows on the skulls of anesthetized dogs. The instrument is sensitive enough to record much lighter stresses. If it can be adapted to problems of chewing stresses in the living, monkeys with split-line patterns similar to those of humans (Henckel, '31) could be used to determine the direction of stresses coinciding with major split-line patterns. In the absence of such work tentative interpretations are presented on the basis of the probable stress systems indicated by the split-lines.

The split-line pattern close to and paralleling the inferior border of the alveolar process of the maxilla, perpendicular to the lines immediately above, was noted by other workers but not explained. Since there are no apparent forces acting in different directions at these adjacents levels, the reason for the striking contrast is not immediately evident. However, the research of Wetzel ('22) gives a clue to the probable response involved. In the alveolar region the periodontal membrane is attached to the cortical alveolar bone. When chewing pressure is applied to a tooth it is driven into the alveolus. This stretches the periodontal membrane and pulls

the walls of the alveolus together on the tooth. At the most inferior portion of the alveolar region the bone is a relatively thin compact layer. In view of the split-line pattern here, it is indicated that the bone is sufficiently deformed so that the principal stress is a bending one, with the axis of the bending paralleling the alveolar margin and the split-lines. The area immediately above is removed from the pull of the periodontal membrane, and so unaffected by it.

If this hypothesis is correct, the organization of the split-lines would make the bending of the alveolar compact bone easier, but would cause less deformation of the Haversian canals. If so, the Haversian system orientation is indicated to be a response to stresses rather than being primarily a strengthening mechanism, as has been suggested by Benninghof ('25). A partial experimental test of the suggested explanation may be possible by obtaining split-line patterns of alveolar margins of teeth that have never been in occlusion, or in which the opposing teeth have been removed. This should give one critical test of the assumption that the split-line patterns are in response to mechanical stresses.

The ascending lines in the alveolar process of the maxilla must be in response to the compressive forces from the tooth row, and thus probably represent areas of pressure. Medially these lines are continuous along the nasal surface and frontal process of the maxilla, as shown in figure 5. This indicates that pressures are transmitted as far as the frontal bone without interruption, although the surface ascending lines conform to the superior border of the piriform aperture and terminate above this opening.

On the other hand, the more lateral ascending lines conforming to the zygomatico-alveolar crest of the maxilla are completely interrupted by the infraorbital system of lines and their continuation through the zygomatic region to the area of origin of the masseter muscle. This indicates that simultaneous tensile forces overcome any upward forces from the tooth row. The tensile force is provided by the temporal and

masseter muscles, with the masseter probably contributing more heavily.

If simultaneous tension overcomes ascending pressures in the infraorbital and zygomatic regions, it follows that no upward pressures from the tooth row ever reach the lateral orbital region. The masseter muscle and some of the anterior fibers of the temporal muscle pull downward upon this region, and the temporal fascia may also contribute. This area is thus probably under tension in chewing, also. This is contradictory to the generally expressed view of anatomists and anthropologists (Weinmann and Sicher, '47; Hooton, '46; Ashley Montagu, '51) that upward pressures from chewing reach the brow region by way of the lateral orbital region.

While the split-lines indicate that the above regions are under tension, the reasons for this conclusion require some discussion. The tooth row receives the combined elevation of masseter, temporal and internal pterygoid muscles, while only the masseter acts with full force to counteract the effects of this upward pressure on the face. However, it is not certain just how efficient the transmission of these muscles forces to the tooth row is (Robinson, '46). The forces are distributed over a fairly wide area by the dentition, though the greatest force is placed upon the first molar (Friel, '24). Some of the pressure goes up through the canine pillar. The curvature of the zygomatico-alveolar process may also help in distributing the upward forces laterally. Finally, the lateral orbital region is lateral to the tooth row, so that forces up to it cannot be transmitted directly. By contrast, the masseter pulls downward directly upon the zygomatic region over a very small area through a tendinous arrangement for the origin of its fibers (Sicher, '49). Temporal muscle fibers also pull directly upon the lateral orbital region as far down as they extend. These factors appear to combine to cause the preponderance of downward forces seen in the lateral orbital and zygomatic regions.

A small portion of the lateral orbital region is below the fibers of origin of the temporal muscle (Sicher, '49). This re-

gion would be under pressure but for the much greater force probably exerted here by the pull of the masseter muscle. Benninghof's ('25) split-line preparations indicate that the temporal muscle exerts its force along the entire length of the temporal lines and within the temporal fossa. Therefore only a relatively small amount of the force of the muscle is exerted directly upon the lateral orbital region. The greater force exerted by the masseter would explain the continuous split-line pattern coursing in that part of the lateral orbital region below the fibers of origin of the temporal muscle.

The dog and cat split-line preparations give the same indications as to the stresses in the region comparable to the lateral orbital, the post-orbital. The split-line pattern deviates into the bony processes giving origin to the tendon-like band of connective tissue which takes the place of a post-orbital bar of bone. Such bands can only resist tension (Weiss, '39), which is provided by the masseter muscle attached below to the zygomatic arch. The split-lines in the post-orbital bony processes must therefore also be responding to tension. The human and chimpanzee stress patterns in this region therefore seem to correspond closely to that indicated for other mammals.

The zygomatic arch shows a longitudinal arrangement of the split-lines. Since the principal force acting upon it is the masseter muscle, it resembles a uniformly loaded horizontal beam supported at both ends. The longitudinal arrangement of the Haversian systems approximates the more flattened of the theoretical trajectories of such a structure and gives considerable resistance to shearing forces exerted by the muscle.

The random split-line pattern of the thin plate of bone forming the posterior wall of the frontal sinus is similar to the lack of orientation in the medial brow region. The superior portion of the canine pillar immediately adjacent is highly organized, the suture line generally marking the break in pattern quite sharply. Here observations on sectioned skulls offer some evidence of what must be taking place. The bone in the canine pillar thickens greatly above the piriform aper-

ture and loses most or all of its cancellation. The frontal process of the maxilla and the adjoining superior portion of the nasal bone have the thickest compact bone observed in the face. The two bones haft to the frontal over a wide area. In 4 specimens sectioned the frontal sinus was immediately above this hafting region, separated from the maxilla by a thin plate of the frontal bone. In the other specimen there was no frontal sinus, the region it usually occupies containing much cancellous bone giving no evidence of trabecular organization.

The above data indicate that the upward pressures in the canine pillar have very little effect on the organization of bone in the brow region. Whatever pressure reaches the frontal is apparently spread over a wide area.

The chimpanzee pattern offers more evidence on the general problem of the relationship of the brow region to the stress systems of the face. The continuous split-lines indicate that the whole area is under tension in chewing. It is thus probably a more extended version of the continuous human system of lines in the lateral brow ridge and lateral orbital region. Since the braincase in this animal is set well behind the orbits, the brow ridges have to take up all the tension from the masseter and temporal muscle without the support of a forehead above. The tensile forces are thus not spread out over a wide area. It may be noted from figure 3 that some human specimens show faint signs of a similar extension of split-lines above the orbits. It seems likely that pressure from the canine pillar of the chimpanzee also has little or no effect upon the organization of the supraorbital torus. Henckel ('31) also observed the sudden breakdown of the ascending pattern at the fronto-nasal suture in man and the chimpanzee.

The split-line patterns of the lower face of the chimpanzee indicate that, as in man, pressures from the dentition never reach the lateral orbital region. Instead of being cut off by a strong system of lines running from the inferior orbital region through the zygoma, however, the chimpanzee ascending lines are gradually bent laterally toward the region of ori-

gin of the masseter. These differences can probably be explained mainly as a function of the different spacial relations between the orbit and the masseter muscle. In the chimpanzee the origin of the anterior tendinous portion of this muscle is relatively much lower and somewhat less lateral to the orbit, corresponding partly with the longer face. As a consequence, the ascending lines come directly into the tensile field caused by the pull of the masseter primarily and the temporal muscle secondarily. On the other hand, the infraorbital lines are cut off from entering this system by being too far above the origin area, and by the lines descending from the lateral orbital region into the zygomatic region.

The progressive looped pattern of the split-lines across the relatively muscle-free zone of flexure between the internal face of the fronto-sphenoidal process and the postero-lateral surface of the orbital process of the zygomatic bone, seen in figure 4, is quite puzzling. Possibly this indicates a region between two areas of downward tension. The former would be from the pull of the temporal muscle in the temporal fossa, the latter mainly from the pull of the masseter. The temporal fascia may also affect this region somewhat.

The preceding discussion of the form and functioning of the human and chimpanzee facial skeletons can be applied to other anthropological problems. For example, the argument over the use of non-adaptive or adaptive characters in primate taxonomy exemplified by Wood Jones ('29a, '29b, '48) and Gregory ('30) is put in clearer perspective if referred to the discussion of Weiss ('49). He shows that the nature of adaptation must be analyzed in every case, because of the broad application of the term. One of the types of adaptation he emphasizes is that of different parts or systems of parts to each other within the individual. Gregory ('30) essentially suggests such internal adaptations for the traits Wood Jones ('29b) puts forth as non-adaptive. The split-lines probably can be used to show when structures of the facial skeleton are built up in response to muscle action, although this remains to be tested experimentally. The absence

of pattern in thickened bone such as the cranial vault, conversely, indicates where the bone development is not a stress response. It cannot, however, demonstrate absence of internal adaptation to other bodily processes.

One anatomical area which has received considerable anthropological attention, the canine fossa, is clarified through split-line analysis of some of these adaptive adjustments within the face. The three divergent systems of split-lines in the human face below the orbits, shown in figure 1, form a rough triangle, surrounding an area which is often relatively unorganized in its split-lines. When this area is recessed it corresponds to the canine fossa. The chimpanzee pattern is one of ascending lines which are diverted laterally, with no relatively unorganized areas in the face. This animal does not have a canine fossa, which is apparently made possible in man because the facial bone may be organized into definite structures associated with the direction of the divergent stress systems indicated by the split-line patterns. The area bounded may or may not have the split-line pattern well organized, and may or may not have thinner bone which is retracted into a fossa, but the essential feature seems to be that the stressed bounding structures must remain relatively thickened while the intermediate region need not. The variability in position or appearance of the fossa may be partly explained when the angles and dimensions of the three stress systems vary in different individuals or groups.

The canine fossa in man thus seems to be a product of the reduction of the face from the probable ancestral condition, with consequently altered muscle relationships and the frequent appearance of the infraorbital bar. It is suggested that the formation of the elevated nasal bridge may also have contributed to this development, creating a medially directed stress system above the nasal opening. No such divergent split-line system is seen in the chimpanzee specimen, where there is no suggestion of elevation of the nasal bones. The elevated nasal bridge itself may be related to the shortening of the face in humans, as Hooton ('46) suggests. Thus a num-

ber of recognizable characters may actually result from adaptation to a single biological process.

The lack of consistent split-line patterns medial to the trigonum supraorbitale in man throws doubt upon the mechanical stress interpretations of large brow ridges, typified by Hooton ('46) and Ashley Montagu ('51). Such doubt is supported by evidence from those cases of acromegaly (Weinmann and Sicher, '47) in which the brow ridges reach formidable size while accompanying overgrowth of the lower jaw prevents chewing altogether. The split-line patterns thus contribute negative evidence on one internal adaptation hypothesis. On the other hand, the strong split-line pattern in the chimpanzee brow region suggests that its form may be influenced by the stresses on the area. Cunningham ('08) observes that the young chimpanzee has a distinct superciliary eminence and a trigonum supraorbitale, but that these become fused and indistinguishable as the animal grows older. As the brow area becomes more separate from the braincase during the growth of the animal, the greater tensile stresses applied more directly to the brow ridges could be enough to require this eventual functional unity. The split-line patterns in the brow region are already beginning to develop in Seipel's ('48) preparation of a three-year-old chimpanzee skull.

It is possible that problems of fossil man may be clarified by comparative split-line data such as that given above for two regions of the face. Neanderthal man may be used as an illustration. Howell ('51) notes that classic Neanderthals contrast with early Neanderthals in having lower cranial vaults, larger facial skeletons, semicircular supraorbital tori of a continuous structure with no distinguishable trigonum, flattened mandibular angle region, shelving of the maxilla into the zygomatic bone with no clear demarcation between the two, and absence of a canine fossa. Howell relates these features to differences in the masticatory muscles in developing his theory of differentiation of classic Neanderthals in western Europe during the Fourth Glacial period. This study

lends support to his suggestion that the features mentioned are interrelated, and suggests possible analysis of other fossil forms.

The classic Neanderthals may represent an intermediate stress condition in the brow region between the chimpanzee and modern man. The low forehead would by this conjecture make necessary a strong reinforcement above the orbits to withstand the pull of the muscles, obliterating the separation between the trigonum area and the superciliary arch but not requiring a continuous torus. The early Neanderthals have a higher vault than these later forms, and show the brow ridge divisions found in modern man. This differs from the interpretation of Howell, who postulates the differences in brow ridges as being related to the differences in relative strength of the masseter muscle, deduced from differences in the malar region.

Howell indicates that a relatively weaker masseter muscle is implied in the formation of the mandibular angle and malar regions of classic Neanderthals. Seipel's ('48) split-line preparations on the angle of the mandible indicate that the effect of the muscle upon the internal architecture and superficial accumulation of the bone is considerable, lending support to Howell's hypothesis. The large face and relatively weak masseter muscle suggest stress relationships similar to those indicated by the split-line pattern of the chimpanzee demonstrated in this study. In both forms there is backward shelving of the malar region and an absence of canine fossa. It is possible that the high, rounded orbits of classic Neanderthals noted by Cameron ('20) are also associated with this masseteric relationship, since there would be less downward pull exerted upon their lateral borders by the muscles. Comparative analysis of form and split-line patterns in contrasting living forms thus tend to support Howell's view that these features are part of a functional complex rather than unrelated structures.

As a cautionary note, however, it must be noted that the presence or absence of a canine fossa may be related to more

than a single cause in different forms. Thus Martin ('28) and Hooton ('46) observe that a canine fossa is rare in Mongoloid skulls. Here the other extreme from the Neanderthal situation is present in the malar region, which is heavily developed and projected forward. If the shelving of the malars is related to the lack of a canine fossa in Neanderthals, different processes are operating to make for its rare appearance in Mongoloids.

The relevance of split-line data to additional anthropological problems has been discussed elsewhere (Tappen, '52). Such discussions will be much more firmly based when the biological meaning of the patterns is established. As has been indicated here, the technique lends itself to combination with comparative studies, developmental analysis, instrumental testing and experimental demonstration on problems of the nature of the Haversian systems and their relationship to observable characters. When such work has been done, the limitations as well as the uses of split-line analysis can be evaluated properly.

SUMMARY

1. Split-line technique was applied to a series of human skulls, a chimpanzee skull, and dog and cat skulls in attempting to clarify anthropological problems of facial form.

2. The split-line patterns of the human face show variability in extent and degree of organization in different regions, but the general outlines are clear. The majority of the patterns can probably be explained in terms of response to mechanical stresses on the bone. They are therefore an index to one kind of internal adaptation and consequent interpretation of the adaptive nature of some of the characters used in classification.

3. While many split-line patterns probably tend to strengthen the bone, their organization is indicated to be a functional response to stress rather than an adaptive strengthening mechanism, from the evidence of split-lines in the inferior border of the maxilla.

4. Split-line patterns of the face indicate that upward chewing pressure in the maxilla is interrupted by tension systems coursing along the inferior border of the orbit and through the zygomatic region, associated mainly with the downward pull of the masseter muscle. The lateral orbital border and lateral portion of the brow region are also regarded as being under downward tension. Comparison with the dog and cat stress situation in the equivalent area tends to verify this. This conclusion is in direct contradiction to the usual anatomical and anthropological interpretations of this region. More centrally, maxillary split-line patterns end along the superior border of the nasal opening, but the deeper system continues in the canine pillar to reach the brow region. The stress situation in the more central brow region remains unclear, since no consistent split-line patterns are observable. The variable situation in the canine fossa region indicates that it is a relatively unstressed area between three divergent stress systems, the infraorbital, zygomatico-alveolar crest, and ascending circumnasal.

5. The chimpanzee differs from man in split-line patterns in several regions. The brow area has continuous patterns indicating that tension from muscle pull operates over the whole torus. This is probably because the braincase does not overlie the brow region to assist in taking up the stresses. Since there is no elevated nasal bridge, the split-line patterns conform to the deeper portions of the canine pillar. In the maxilla, ascending split-lines are uniformly deviated laterally by the pull of the chewing muscles. There is thus no region between strongly stressed systems in the face to correspond to the canine fossa region of man. The chimpanzee infraorbital split-lines are not continuous with the zygomatic origin of the masseter muscle. They are cut off by vertical lines associated with the lateral orbital boundary. The differences from the human pattern are probably a function of the relatively lower origin of the masseter muscle. The absence of a canine fossa in the chimpanzee is probably associated with this stress pattern.

6. Sections of human skulls show that most thickened areas of bone are accompanied by strong split-line systems, indicating adaptation of the thickened structures to mechanical stresses. A notable exception is the central brow region, where thickened bone shows no consistent split-line patterns. Here the form probably does not represent a response to mechanical stresses. This indicates that stress resistance is not a primary function of human brow ridges although in many primate forms they undoubtedly become involved in facial stress systems.

7. The interpretations of split-line patterns made in this study, and their anthropological applications, can in general be evaluated through instrumental tests, developmental analyses, comparative studies and experimental demonstrations. Because of the ready combination of split-line technique with these other methods it should contribute much more to solution of anthropological problems.

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BODY WEIGHT, RACE AND CLIMATE

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EIGHT FIGURES

Examination of heat production in indigenous peoples by reference to the climates of their habitats (Roberts, '52a, '52b) suggested that a relationship existed between body weight and mean environmental temperature. Further investigation of this suggestion forms the subject of the present study. The problem may be stated as follows: Does mean body weight vary with mean annual temperature, and is any racial influence evidenced?

Data were obtained from the literature.[1] The first main source was the large number of papers giving metrical information about human groups. Unfortunately, in these "racial" studies, with their objective of classification and the consequent neglect of the more variable body features, weight data are rarely to be found: for example, to obtain the 28 comparable African samples here used, 4 of which are not yet published, it was necessary to examine nearly 750 series of African measurements, an incidence of slightly more than 3%. However, when weight details are included in anthropometric studies, the sample may usually be regarded as of adequate size and as representative of the population. The second source of data was furnished by reports devoted to the examination of particular physiological problems. These

[1] I should like to express my thanks to Dr. J. Hiernaux, at the Institut Royal des Sciences Naturelles, Belgium, for making available to me his unpublished figures for weights in Ruanda Urundi; to Mr. J. Harries and Miss D. Hollingsworth of the Ministry of Food, London, for allowing me access to their data; and to Dr. J. S. Weiner for the stimulus of numerous discussions and for his valuable criticism of the text.

generally refer to smaller numbers of individuals, the samples are rarely drawn at random from the population but include those subjects who are available at the laboratory or hospital, the provenance of the subjects is often omitted, and their racial affinities are but loosely described. Publications of both types were reviewed and, in all, data were collected relating to more than 220 adult male and fewer female samples drawn from indigenous populations in many parts of the world (excluding European residents outside Europe).

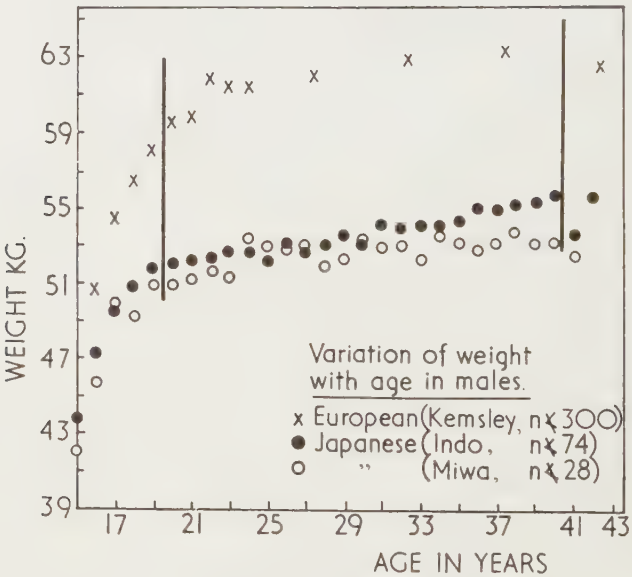

Fig. 1 Variation of weight with age in males.

From this assemblage of data were obtained series which could be regarded as comparable when due consideration was given to the factors known to influence body weight.

Error due to misprints was minimized by obtaining figures in every instance from original sources. Mean values were used. No sample was included of fewer than 20 individuals, sample size thus varying between 20 and about 3,000; the lower limit was determined after consideration of such data as were available for weight variability, standard de-

viations in the present series ranging from 3.78 to 9.4 kg and averaging 6.72 kg. All sexually heterogeneous samples were rejected, and samples for each sex dealt with separately. It was obviously necessary to consider carefully the age composition of the samples; the relatively slight rise *(circa* 4 kg) in mean weight between the ages of 20 and 40 in European populations (Kemsley, '50) and its apparent parallel in other human populations (e.g. in Japanese, Indo and Miwa, '13), shown in figure 1, seemed to justify the selection of these age limits; all samples containing individuals of less than 20 years of age, and samples whose mean age fell above the upper limit, were excluded. The immediate effects of disease may be discounted, since only healthy individuals were included in the groups considered, although it was impossible to estimate the effect of previous diseases. Ensuring that samples were indeed representative of their parent populations was impossible; all that could be done was to reject, where the relevant information was given, those samples socially or occupationally selected (e.g. labor recruits) and thus diminish, not eliminate, error on this score. The influence of clothing was almost eliminated by the use in most instances of nude weights. Although variation due to season, the time of day at which the observations were taken, the length of time since the last meal, diet, quality and quantity of the food supply, habits and occupation, could not be eliminated, these factors should be borne in mind.

In short, of the factors known to influence weight, an attempt was made to reduce the number operating upon the data here considered by rejecting all questionable samples; it is unfortunate that so few factors could be eliminated.

Subsequent to this preliminary assessment of the material, there remained 116 male and 33 female samples which seemed sufficiently comparable for statistical examination, and rather more groups whose weight could be mapped, representing populations of many races, of all major human varieties, from many parts of the world.

GEOGRAPHICAL DISTRIBUTION OF BODY WEIGHT

General

The geographical distribution of the series of 116 male mean body weights chosen for statistical examination is shown in the sketch map (fig. 2). There is apparent a marked tendency for most "very high" weights to occur in cold areas and for "very low" weights in hotter regions.

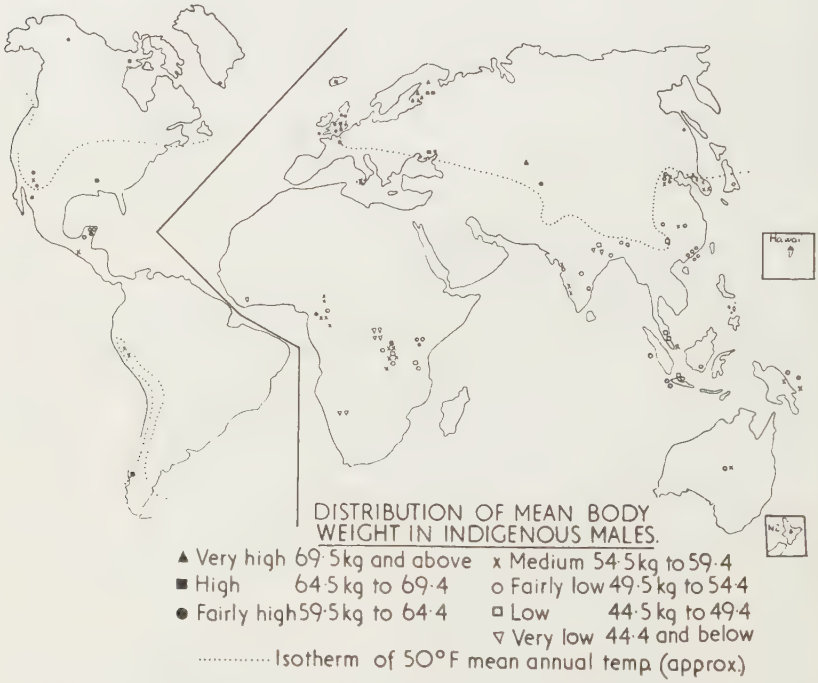

Fig. 2 Distribution of mean body weight in indigenous males.

"Medium" weights occur at all latitudes from 0° to 40°, while weights above average preponderate in more temperate and cooler regions, those below average in warmer areas. A temperature relationship is clearly demonstrated by reference to the isotherms of mean annual temperature, one of which (that for 50°F.) is indicated on the diagram; very few of the samples in the categories heavier than medium fall to

the warmer side, and only one sample lighter than medium falls on the cooler side, of this isotherm.

A temperature relationship also appears to exist within continental groups. In Europe and eastern Asia weights tend to increase from warmer south to cooler north. In America the gradient of weight from cold to hot areas is somewhat

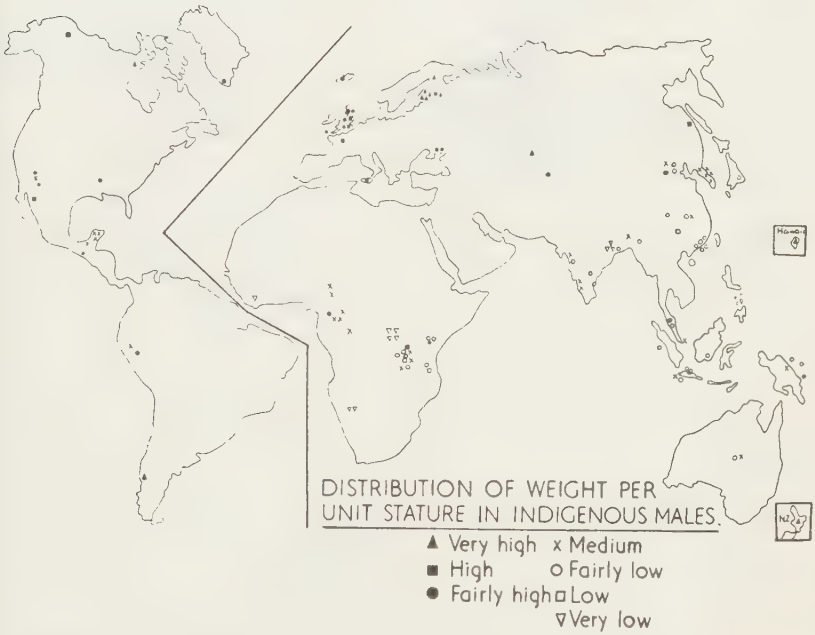

Fig. 3 Distribution of weight per unit stature in indigenous males.

less clear, largely on account of the high figure for the Choctaw. For African groups, the mean environmental temperatures cover a smaller range, some 17°F.; comparison of racially and culturally similar groups, e.g. Ituri Bambuti with Ruanda Batwa, Bahutu at low medium and high altitudes, suggests weight variation either with altitude or concomitantly temperature.

Differences are also suggested among continental groups. In Oceania, Polynesians seem to be characterized by higher weights than Melanesians. Europeans appear to be heavier

than East Mongoloids at similar temperatures. It is difficult to identify the effects on body weight of economy (e.g. pastoral Batutsi and cultivating Bahutu are both of medium weight, but pastoral Masai are heavier than the nearby Kikuyu cultivators). Occupation seems to exert some influence: e.g. when the sample of Chinese at Changsha is subdivided into occupation groups, heavier weights tend to occur

Fig. 4 Weights of Bantu mineworkers at Johannesburg according to area of origin (figures of Brodie and Turner). All samples over 25 in number.

in the more laborious occupation groups and among students; samples from Pekin support this suggestion.

In short, examination of the distribution of mean body weight in indigenous male groups suggests that, although minor variations due to occupation and several other factors may occur, there is an underlying inverse relationship between weight and mean environmental temperature discernible not only when all mankind is considered but also within

continental groups of man, and that differences in level occur among continental groups.

The same general pattern appeared when weights expressed per unit stature were mapped (fig. 3).

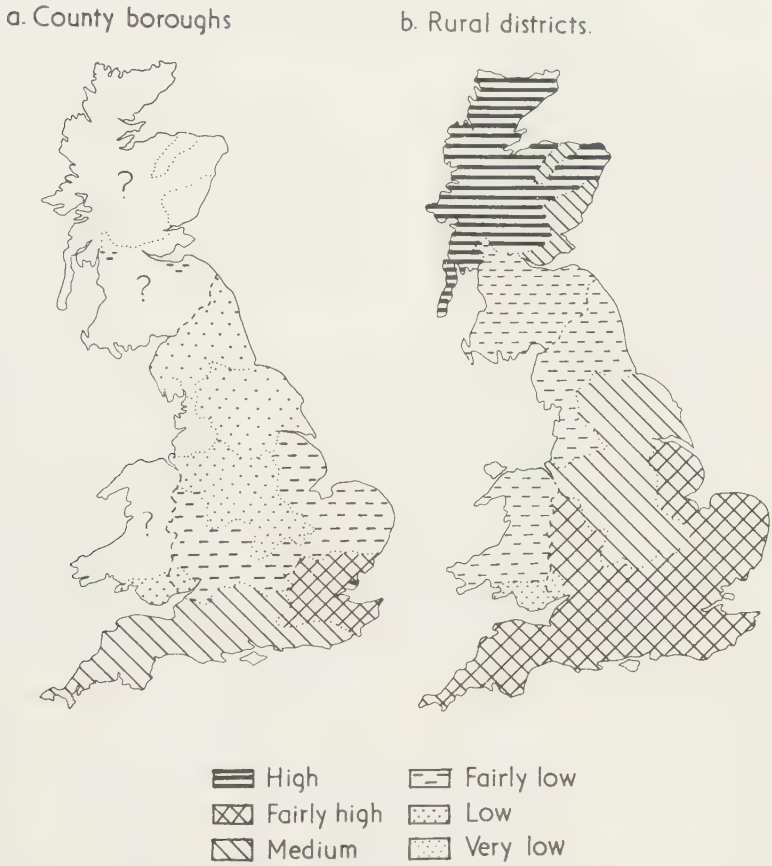

Fig. 5 Mean weights, young men aged 20–21.

Regional

For a few regions more detailed information is available. There are a number of observations of southern Africans at the mines at which they worked, obtained by Brodie and Turner, both unpublished. The numbers of individuals are

large — Brodie measured 3,339, Turner 604 — and were drawn from several tribes. These samples were not included in the examination of other African groups living under tribal conditions since they were quite heavily selected by age, physique and several other qualities, besides living conditions and diet.

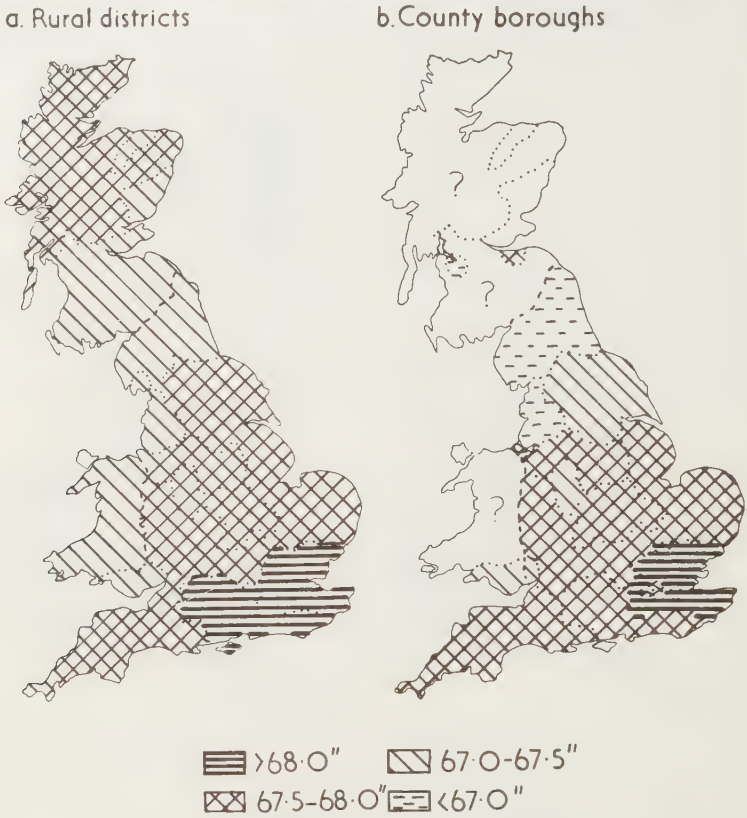

Fig. 6 Mean stature, young men aged 20–21.

The effect of this selection was assumed to be constant on all groups of mineworkers. The weights of samples containing 25 or more individuals were plotted according to the area from which they were recruited. The sketch (fig. 4) shows that weights of Bantu mineworkers are in agreement with the findings of the general survey, in that higher weights tend to occur in cooler, and lower in warmer, areas.

As an example from an area with a small range of mean temperature, a representative cross-section of the population of Britain is afforded by the large number of young men, all between the ages of 20 and 21, measured in 1939 (Martin, '49). Weights for rural groups, when plotted (fig. 5 b), show that heaviest people occur in the Scottish highlands and Cornwall, lightest in South Wales, and that otherwise a marked gradient can be perceived which, passing from heavier means in the south and east to lighter in the north and west, is not in accordance with the slight temperature differences. Weights for samples from county boroughs (fig. 5 a) show a similar gradient, but these urban populations are all lighter in weight than their rural neighbors.

The distribution of stature for these samples shows a similar pattern, there being again a diminution northwards and westwards (save for the Scottish highlands), and again a tendency for values to be lower in urban than in rural communities (figs. 6 a and 6 b). Hence it is suggested that to variations in stature, whatever their cause, may be attributed a certain proportion of the regional variation in weight in Britain; a similar conclusion is reached from examination of regional variation in weight in Finland (figures are given in Suominen, '29).

That stature is not the only determining factor, however, is shown by comparison of groups of identical height. For example, samples from county boroughs in the Wiltshire/Sussex and Shropshire/Bedfordshire regions both have the same mean height of 67.8″ but the former is 3.3 lb heavier; county boroughs in the Southwest, East Anglia, and Warwickshire, have average statures of 67.5″ but the first sample is more than 2 lb heavier than the other two; rural districts both of Glamorgan and the 4 northern counties have mean heights of 76.2″, but the former is 2.7 lb lighter than the latter; rural districts in Leicestershire/Northamptonshire share with the Scottish highlands a mean stature of 67.8″ but the latter is more than 5 lb heavier. Clearly, though the last

two comparisons may reflect a temperature influence, such may not be postulated for the first two comparisons.

Examination then of series drawn from regions of more limited environmental range shows that the expected small effect of the climatic factor in these instances may be obscured by relatively greater variation in a number of other influences — a possible reason for the overlooking of "large-scale" geographical relationships of weight in the past. Of these other influences, stature would appear to be predominant; the other factors it is difficult at the moment to identify.

STATISTICAL RESULTS

Evaluation of the suggested relationships by statistical methods was accordingly undertaken. The series of samples used is given in the appendix. Mean temperature figures were obtained for each locality from which the samples had been drawn, from local meteorological records where available, but otherwise by interpolation from the nearest stations.

First, the significance of the association between mean weight and mean annual temperature was examined (fig. 7). When all comparable 116 male samples were considered, the correlation coefficient $r = -.600$ resulted, highly significant at 0.1%; the relationship appearing linear, a regression line of weight on temperature was fitted by the method of least squares with a value for the regression coefficient $b = -.305$ (kilograms per degree Fahrenheit). Thus the inverse relationship between weight and environmental temperature, postulated from examination of the geographical distribution, is supported by statistical analysis.

To clarify further this apparent relationship it was necessary to take into account stature which was obviously responsible for a certain amount of variation. The question was whether the lower weights of tropical, and the higher weights of temperate, dwellers were due to respectively smaller and greater statures, for in the present series of samples a significant relationship appeared between stature and temperature ($r = -.351$, significant at 0.1%) and the correlation

coefficient between stature and weight was $r = +.734$, highly significant at 0.1%. The partial correlation coefficients were therefore calculated. The high correlation between weight

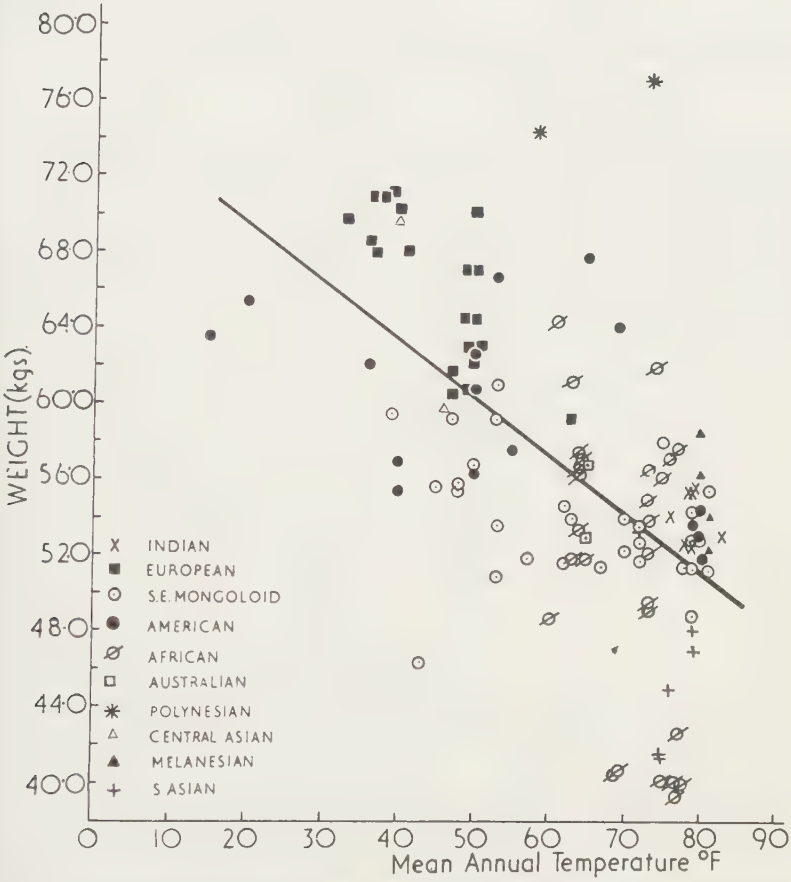

Fig. 7 Relationship of weight and mean annual temperature. Male indigenous groups.

and stature exclusive of temperature was again highly significant at 0.1% with the value $r_{ws.t} = +.698$; the high correlation between weight and temperature exclusive of stature remained highly significant at 0.1% ($r_{wt.s} = -.538$), and the correlation between stature and temperature disappeared

($r_{st.w} = +.164$, not significant). The multiple correlation coefficient, $R = .820$, indicates the importance of stature and temperature in affecting the weight of a sample, seven-tenths of the total variance in weight thus being ascribable to these two factors. Both partial regression coefficients being highly significant, the "prediction" formula for mean body weight may be expressed

$$W = .071S - .199T - 48.1$$

where W is the mean body weight in kilograms, S is stature in millimeters, and T is mean annual temperature in degrees Fahrenheit. Mean weight then apparently decreases by a kilogram with an increase in temperature of 5°F., but increases by a kilogram with an increase in stature of approximately 1.4 cm.

TABLE 1

Correlation coefficients in the female series

	TOTAL CORRELATION COEFFICIENT	SIGNIFICANT AT	PARTIAL CORRELATION COEFFICIENT	SIGNIFICANT AT
Weight and stature	+.813	0.1%	+.712	0.1%
Weight and temperature	—.809	0.1%	—.704	0.1%
Stature and temperature	—.587	0.1%	+.208	not

The use of a cubic function in the comparison of weight and stature has been advocated by a number of authors, e.g. Livi (1898), and Gavan ('52). Would the relationship have been different if stature had been expressed in terms of its third rather than its first power? Calculation of the total correlation coefficients in these terms produced no significant difference from those stated above; the correlation coefficient between weight and stature cubed was $r = +.742$, between temperature and stature cubed $r = -.360$, and the multiple correlation coefficient $R = .823$. Hence it was not incorrect to use stature to the first power during the present calculations.

By way of confirmation of the foregoing relationships, similar calculations were performed on the short series of female samples available, 33 in all, giving the results shown in table

1; there is general concordance between the results for the two sexes.

The samples having been drawn from all varieties of man it was necessary to enquire whether any variation in body weight could be associated with or attributed to the fact that a particular sample was drawn from a particular variety of man. For this purpose covariance analysis was applied to the data.

The samples were assigned to the following 10 varieties or geographical groups: American, all samples drawn from native Indian and Eskimo populations of that continent; African, all samples examined in that continent south of the Sahara, including Pygmy and Bushman; East Mongoloid, samples of Mongoloid affinities from east and south Asia, i.e. excluding populations of India and aboriginals of Malaya, but including Indonesian groups; Central Asian, the samples from that region of Kazak and Kirghiz; South Asian, non-Mongoloid primitive groups, aboriginals of Malaya and eastern India; Indian, all samples from that subcontinent save the aboriginals; European, peoples in that continent; Australian, aboriginal samples; Polynesian, samples of Maori and Hawaiians; Melanesian, samples from that region. The basis of the grouping was geographical, but a tentative anthropological classification was incorporated, the aim being that any sample within a group should possess more features in common with its companions in that group than with any sample in any other group. To anticipate criticism of this system, some of the more striking departures may perhaps be commented upon. Bushmen were included in the African group since their exclusion would have necessitated similar treatment of the Sandawe, who, though possessing a number of traits in common with the Bushmen, also show affinities with neighboring Bantu-speaking groups. Eskimo were assigned to the American category since they may not be incorporated in any of the others here used, a classification with which known gene frequencies of other Eskimo samples appear to agree. Details of the racial composition of Indian town samples were al-

most completely lacking so that a continental description distinct from the other groups seemed the obvious solution.

It is when such a classification is attempted that the inadequacy of available material is most realized. Lack of genetic information of the samples precludes accurate genetic classification, an essential preliminary to the assessment of environmental influence. The small number of samples tends to lead to the use of too-inclusive categories, or categories

TABLE 2

Analysis of variance

SOURCE	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	
Total	115	715714		
Within groups	106	275878	2602.6	F = 18.78 significant at 0.1%
Among groups	9	439836	48870.7	

TABLE 3

Analysis of covariance: comparison of adjusted means. Errors of estimate

SOURCE	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	
Total	113	234809		
Within groups	104	119345	1147.5	F = 11.18 significant at 0.1%
Among groups	9	115464	12829.3	

containing too few results, both of which may well render indistinct any existing relationships. It was thought better, however, to err in this direction rather than the contrary.

First, were there significant differences among the weights of the 10 groups? Analysis of variance given in table 2 showed that such differences were highly significant, at 0.1%, indicating that some of the groups possessed greater weights than others.

Were these differences attributable to variations in features shown to be associated with weight, viz. temperature

or stature? Covariance analysis, given in table 3, indicated that differences among adjusted means of the groups were highly significant at 0.1%, i.e. that intrinsic differences in weight existed among the groups after allowance was made for the association with stature and temperature. Calculation of the adjusted means of the groups produced the interesting results shown in table 4, that the lowest weights occurred among groups thought to have occupied a tropical habitat for a considerable time, South Asian and Australian aboriginal and African populations. The proximity of Indian and East Mongoloid results is worth notice, and so is the position of American, European, and Central Asian groups

TABLE 4

Mean weights of groups adjusted for temperature and stature arranged in increasing order

	kg		*kg*
South Asian	51.79	Melanesian	59.84
Australian	51.90	American	59.92
African	53.92	European	59.93
Indian	54.52	Central Asian	62.20
East Mongoloid	54.69	Polynesian	71.82

at the upper end of the scale. For interpretation of Melanesian and Polynesian figures it is necessary to await further evidence since the groups contain respectively 4 and two samples.

Moreover, this analysis demonstrated that the relationship of weight with temperature and stature also occurred within groups, i.e. remained after allowance was made for the differences among groups. Within groups, the total correlation coefficient between weight and temperature remained highly significant (at 0.1%) with the value $r = -.362$; that between weight and stature was again highly significant (at 0.1%) with the value $r = +.711$; but that between stature and temperature disappeared ($r = -.166$, not significant). Calculation of the within group partial correlation coefficients produced similar results; that between weight and temperature

exclusive of stature ($r_{wt.s} = -.352$) was highly significant at 0.1%; that between weight and stature exclusive of temperature ($r_{ws.t} = +.712$) was highly significant at 0.1%, while there was again no correlation between stature and temperature exclusive of weight ($r_{st.w} = +.160$, not significant). The within group multiple correlation coefficient was calculated to be $R = .753$.

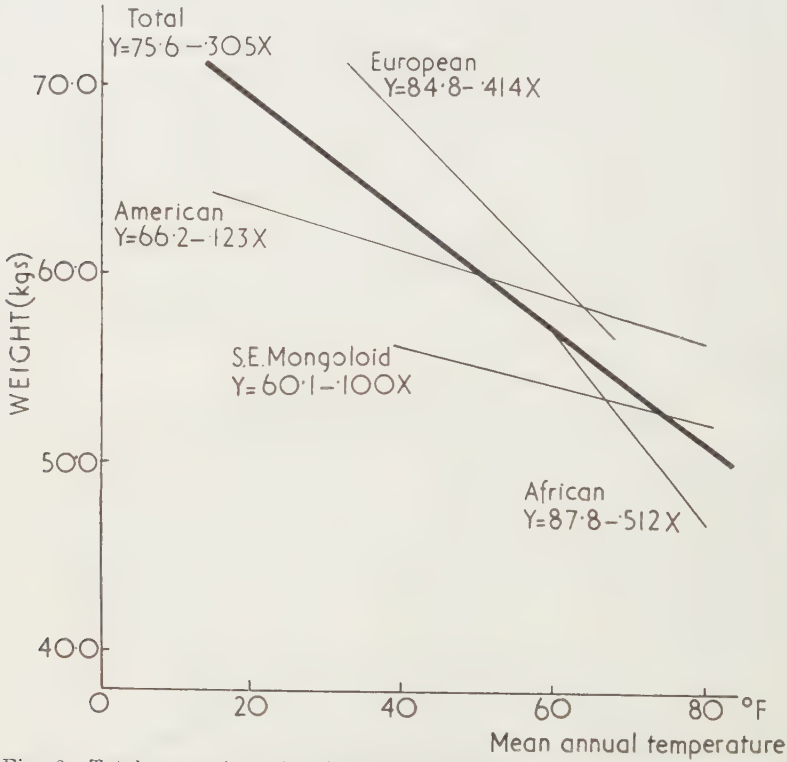

Fig. 8 Total regression of weight upon mean temperature, and some of its component intravarietal regresssions.

Nor did the use of stature expressed to the third power instead of the first appreciably alter these findings. The total correlation coefficient of stature cubed with weight was $r = +.716$ (significant at 0.1%), with temperature $r = -.163$ (not significant); the differences between adjusted means were again highly significant at 0.1% as is shown in table 5.

Only 4 groups contained sufficient samples to allow any attempt at the evaluation of individual within group correlations (see fig. 8); total correlation coefficients are shown in table 6.

TABLE 5

Analysis of covariance: comparison of adjusted means. Errors of estimate

SOURCE	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	
Total	113	230388		
Error	104	119069	1144.9	F = 10.80 significant at 0.1%
Between groups	9	111319	12368.8	

TABLE 6

Intra-group correlations

	NO. OF SAMPLES	WEIGHT/ TEMPERATURE	SIGNIFICANT AT	WEIGHT/ STATURE	SIGNIFICANT AT
African	28	—.395	5%	+.852	0.1%
American	16	—.493	10%	+.818	0.1%
East Mongoloid	29	—.421	5%	+.357	10%
European	20	—.755	0.1%	+.450	5%

DISCUSSION

Statistical examination of the data then appears to confirm the inferences drawn from general geographical considerations. The inverse relationship postulated between the mean weight of human groups and mean temperature is seen to be an actual relationship rather than a pattern due to any chance selection of the data. The depression of mean weights in tropical areas, and their elevation in cooler areas, is seen to be accounted for in part by the affinities of the samples with particular racial or geographical groups, in part by a tendency within such groups. Variation of weight with stature, marked though it be, seems scarcely to affect the temperature relationship; that is to say that the weight of a group is influenced by the temperature of its habitat, stature merely inducing additional variation. Other factors may well be operative, as the sketch maps suggested, but the ex-

tent of their influence, including that of chance effects, is not greater than would account for three-tenths of the total variance of the series here examined. It should perhaps be noted that the overall correlation of stature and temperature in the present series, which disappeared in the within-group calculations and hence may be considered due to the differences in stature among the different continental groups here used, was tested on a longer series of samples (between 300 and 400) and found to be absent.

The need for caution in the interpretation of the results, on account of the limitations of the data used, must be stressed. The number of samples included is admittedly small; the blame for this should be laid on those responsible for directing past anthropometric investigations who have overlooked the value of weight as a descriptive character, one moreover not difficult technically to obtain. The use, dictated by the availability of records, of mean annual temperature instead of some physiologically more meaningful climatic measure could doubtless be improved upon. Hence no claim is made to finality, but the results to date seem to be of sufficient interest to be put on record.

What meaning is to be attached to the relationship of weight of indigenous peoples with temperature? Three possibilities may be suggested:

1. It may indicate, for a given stature, a different distribution within the body of the body mass, a different morphology. It can be easily shown that for a given stature a lower weight at increased temperature gives an advantageous ratio of body surface area to mass, thereby facilitating the *maintenance of the body heat balance.*

2. In the course of examination of the relationship of basal heat production with environmental temperature (Roberts, 52b), the following interesting fact emerged: there was a high correlation between weight and temperature ($r_{tw} = -.573$) which remained highly significant ($r_{tw.s} = -.584$) when allowance was made for the association of weight with stature, but which disappeared ($r_{tw.sh} = +.155$, not significant) when

allowance was made for the influence of stature and heat production. Hence it seems reasonable to infer that the weight/temperature relationship may exist as an aid in the *adjustment of body heat production* to environmental conditions.

3. It may include a tendency in cold climates for greater amounts of fat to occur subcutaneously which, from its insulating properties, would appreciably affect *body heat loss.*

Each or all of these suggestions may be contributory. It would clearly be of interest to investigate the body composition of indigenous peoples, to enquire whether it is the lean body mass instead of overall weight which is associated with climate.[2] Again it would not be difficult to include measurements of skin thickness, and the bodily distribution of its variations, in anthropological surveys. Until data of this type are forthcoming, little more can be said concerning the ecological significance of the weight/temperature relationship, save that possession of lower weights in warmer, and greater in cooler, areas may well be advantageous.

The weight/temperature relationships here demonstrated suggest that Bergmann's rule (that within a polytypic warm-blooded species, the body size of a subspecies usually increases with decreasing mean temperature of its habitat), is applicable to man. Clearer definition of "body size" is, however, necessary. Defined by reference to stature, although from the series here considered Bergmann's rule might seem to be applicable, this suggestion is refuted by more extensive material. Defined by weight, it is not only applicable but needs restatement to incorporate, with the postulated variation in size among subspecies, similar variation within the subspecies.

The present data are not adequate to show whether the relationship between weight and temperature is direct or in-

[2] It is not legitimate at the present stage to extend the prediction formula, obtained by Miller and Blyth ('52) for lean body mass from oxygen consumption, to non-European populations living in different climates; should however the application of this formula to indigenous peoples prove to be valid, it would suggest that lean body mass per unit weight decreases with increased temperature, or in other words that in colder climates the proportion of metabolically active tissue to inert tissue is higher than in warm climates.

direct, in the former case constituting an immediate response to temperature, in the latter acting through the intermediaries of type and amount of food supply, habits, genetics, etc. If it is indeed advantageous in warmer areas to possess lower weights, then providing that condition is attained it would appear immaterial whether achieved directly or indirectly.

If, at the moment, it appears profitless to speculate on the degree of causality of the relationship, it may be pointed out that all responsibility should not be attributed to nutrition, for this would render difficult of explanation a number of features, e.g. the European correlation, the high non-European cold results, and the low figures of adequately-fed tropical dwellers. It is interesting that the lowest weights do not appear in areas of greatest population pressure, nor do the highest always occur where living conditions are easiest. Further, if nutrition were the cause, one might expect a certain nutritional influence during the growing period, affecting for example stature; elimination of the stature factor then should markedly reduce the correlation between weight and temperature, which clearly does not occur.

The impression received during the course of the present study is that there is a general weight level for given climatic conditions about which actual weights vary according to socio-economic and nutritional standards. Could there be a genetic factor involved in such a general weight level?

To prove this suggestion, to assess quantitatively the relative importance of genetic and long- and short-term phenotypic influences, is at the moment impossible. The evidence, however, at least suggests that some genetic factor is operating:

1. Studies of twins have shown (Newman, '42) that more than 75% of observed variability in weight may be attributed to genetic influence.

2. In America (Meredith, '52), mean weight of viable Negro infants at birth was about 4% lighter than that of American White infants living in the same area; further, between Negro and White infants receiving adequate dietary and

medical care, there was no difference in mean stature at ages of 6 months, 9 months, and 12 months, but White infants were slightly heavier at each age.

3. As compared with temperate groups, lighter weights for given statures in long-established tropical populations have been reported at all ages, e.g. in West African boys from 10 to 18 years (Weiner and Thambipillai, '52), in aboriginals of Bihar from 7 to 15 years (Majumdar, '52); however the Polynesians (Wissler, '30) and Micronesians (Greulich, '51) appear to possess greater weights for their stature and age than other tropical dwellers. Each of these facts would be expected were the weights of indigenous groups genetically adjusted over a period of time to their environments.

4. The extent of the short-period phenotypic effects of temperature and calorie intake may be roughly estimated by further analysis of the fluctuations in Britain between 1943 and 1949 of weights (Kemsley, '50, '52), of food consumption (Harries and Hollingsworth, '53) and of temperature. Regressions of weight on these variables were calculated, and the results were applied to the weight/temperature relationship found in the present study. The short-period temperature effect, exclusive of food intake, appears to account for only one-eighth of the overall world depression in weight with increased temperature; further, the differences in calorie intake, exclusive of temperature, required to account for the remaining seven-eighths are considerably greater than those observed in nutritional studies to date. Although, in view of the crudity of the procedure, no great stress should be laid on these findings, they seem to suggest that effects of differences of food intake and temperature such as operate in short-term weight fluctuations are only partly, if at all, responsible for the geographical pattern of body weight shown in this survey.

As regards the material used in the present study, it is interesting that, wherever an equatorial sample is designated as representing the aboriginal population of an area, its weight is lower than that of later comers, e.g. the aboriginal Orang Balik Papan of Borneo have a mean weight of

about 46 kg whereas later immigrants vary about 51 kg, the Senoid peoples of the Malayan interior vary between 45 and 48 kg whereas the Malays vary about 52 to 55 kg, the Santals and Paharias of Bihar vary between 41 to 45 kg while later comers vary about 52 to 55 kg. A certain proportion of this depression may be accounted for by the different way of life and less opportunity to take as full advantage of their surroundings as the newcomers, who would tend to choose the more favorable areas; however, in view of the findings of the present study it may perhaps be suggested that at least part of this depression may be due to the longer period over which any selective advantages conferred by lower weight might have operated. Unfortunately this argument may not yet be supported by application to aboriginal inhabitants of cold areas since there are at present no data. It is moreover possible to interpret the significant differences between adjusted means (table 4) as being in accordance with genetic influence upon weight; it is however equally possible to interpret them as reflecting some other as yet unanalyzed influence, e.g. habits, or they may in fact be due to a curvilinear relationship between weight and temperature, rather than linear. Final judgment is impossible in view of the lack of genetic, nutritional, and other necessary information.

Whatever the solution to the question of directness of response, which future work alone can decide, there is one implication clearly carried by the present study. There is a relationship between mean weight and environmental temperature. There should therefore no longer be talk of universal "norms" of weight based upon European standards, to be applied indiscriminately in nutrition and growth studies of other races in other parts of the world.

SUMMARY

The geographical distribution of mean body weight in indigenous populations suggests an inverse relationship with mean environmental temperature. Statistical analysis showed this association to be highly significant, both before and after

the influences of stature and group affinity were taken into account. There are differences in weight among geographical groups or varieties of man, not attributable to the temperature and stature relationships.

The ecological significance of the results is discussed, and some genetic influence suggested.

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APPEDIX A

Samples used in the statistical examination

GROUP	NO. IN SAMPLE	WEIGHT	STATURE
		kg	*cm*
African			
Kikuyu	436	51.9	164.6
Masai	76	61.3	172.0
Sandawe	100	49.4	164.6
Nyaturu	50	52.2	165.4
Pygmy	111	40.1	142.2
Pygmy	36	39.3	142.2
Bushman	34	40.4	156.4
Bushman	54	40.4	155.4
Kikuyu	100	51.8	164.0
Gagou	24	42.6	159.3
Efe	386	39.8	143.8
Akka	115	40.0	144.4
Djem	100	56.6	162.9
Dzimou	83	57.7	163.4
Yambasa	248	62.0	169.0
Badjoue	200	55.0	166.6
Baya	412	53.9	163.0
Kirdi	332	56.2	165.8
Kirdi	549	58.0	167.0
Batutsi	177	57.4	176.5
Batutsi	119	56.3	175.2
Bakiga	70	64.5	168.4
Bahutu	184	57.5	167.1
Bahutu	216	56.7	165.9
Imbo	28	49.5	161.3
Batwa	113	48.7	155.3
Bashi	108	53.5	163.9
Warega	100	57.2	162.1
Australian			
Central tribes	20	53.1	169.7
Central tribes	27	56.9	168.7
Melanesian			
Jabim	26	56.4	161.0
Aua	29	54.3	157.1
Massawa	49	58.7	160.5
Mira	20	53.1	161.5
American			
Eskimo	30	65.3	162.7
Maya Quiche	30	57.6	159.3
Mapuche	31	66.8	163.3
Maya	24	52.4	158.0
Maya	30	54.4	156.0

APPENDIX A *(continued)*

GROUP	NO. IN SAMPLE	WEIGHT	STATURE
		kg	*cm*
Maya	32	53.1	157.3
Choctaw	33	67.8	171.4
Yaqui	100	64.0	166.7
Zuni	348	56.3	161.4
Hopi	276	60.8	161.1
Navaho	125	62.7	169.6
Peru	many	55.5	159.0
Peru	many	56.8	159.0
Maya	70	53.7	156.4
Eskimo	121	62.1	159.3
Eskimo	39	63.5	165.7
European			
Greek	80	64.4	164.8
Sicily	29	59.2	162.4
England	3000	64.5	166.3
Iceland	652	68.1	173.6
London	46	70.1	179.4
Kainuu	many	69.8	170.4
Pohjanmaa	many	71.0	171.9
Häma	many	71.0	171.7
Savo	many	68.0	169.6
Karjala	many	68.6	169.7
Varsinais	many	71.3	172.5
Uusimaa	many	70.3	171.4
London	many	62.2	172.2
Edinburgh	many	61.8	170.4
Glasgow	many	60.5	169.4
Southeast England	many	63.0	173.0
Cornwall	many	63.0	171.7
Staffordshire	many	60.8	170.9
Paris	2619	67.0	172.5
Bulgars	121	67.1	167.2
Central Asian			
Kirghiz	40	59.7	165.3
Kazak	30	69.7	163.1
East Mongoloid			
Javanese	24	48.9	163.6
Javanese	33	52.9	164.3
Malay	50	55.5	166.4
Banjerese	35	51.3	157.0
Sundanese	37	54.4	159.1
Sundanese	200	51.4	159.9
Mentawei	202	51.5	156.5
Filipino	88	53.0	163.0

APPENDIX A *(continued)*

GROUP	NO. IN SAMPLE	WEIGHT	STATURE
		kg	*cm*
Pekin	49	59.2	169.3
Pekin	34	53.6	167.2
Hongkong	87	52.7	166.0
Szechwan	54	51.7	165.0
Miao	24	46.4	154.0
Japanese	42	51.9	161.9
North China		61.0	168.0
Central China	351	54.0	165.0
South China		54.0	165.0
South China	30	52.3	163.4
North China	23	50.9	159.0
Central China	328	54.7	163.0
Hongkong	115	51.8	166.3
Korea (Chung Chong)	27	55.8	161.3
Korea (Kyong Kwi)	354	55.5	161.1
Korea (Hwanhai)	22	55.6	160.3
Korea (Pjonjan)	45	56.8	163.0
Korea	594	59.2	163.2
Hoklo	117	53.6	162.7
Orochee	93	59.5	155.0
Naga	33	51.5	160.3
Polynesian			
Maori	384	74.5	170.6
Hawaii	60	77.3	171.3
South Asian			
Santal	313	45.0	159.3
Malpaharia	60	41.6	156.3
Sauriapaharia	69	41.4	156.2
Mande	23	53.6	158.8
Senoi	39	48.1	156.4
Senoi	39	47.0	154.6
Indian			
Bengal	1193	52.7	165.8
Brahmin	100	55.5	163.8
Mahratta	162	55.7	163.8
Bombay	60	55.5	167.9
Hyderabad	32	54.2	169.3
Bombay	24	52.5	166.0
Madras	61	53.1	167.0

VARIATIONS IN URINARY EXCRETION PATTERNS IN A TEXAS POPULATION [1]

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The relative abundance of data on the variability of morphological traits in most diverse human populations contrasts strongly with the scarcity of reliable information on physiological and biochemical traits. With the exception of the blood antigens which have been extensively studied in recent decades, biochemical characteristics are still largely ignored as materials for anthropological studies. And yet the work of physiologists and biochemists has disclosed a very considerable variability among human subjects, both in good health and in disease, affecting particularly the metabolic patterns. As pointed out especially by Williams ('46), it is justified to speak of biochemical or metabolic individuality, which is perhaps no less pronounced within the human species than the morphological individuality, although the latter is more easily apprehended by superficial observation. The recent developments of analytical techniques of partition chromatography on paper furnish rapid, inexpensive and reasonably easy and precise methods for studies on biochemical individuality in human

[1] This work was supported in part by a grant from the Office of Naval Research. The author wishes to acknowledge the interest and aid of Dr. Roger J. Williams in the course of the work. The major portion of the data assembled here have been collected over a period of years by many people working in the Biochemical Institute under Dr. Williams' general direction. These, in addition to the author, include Kendall Young, Jack Brown, Janet Reed, Duane Brown, Richard Pelton, Louise Cain, Lyman Ripperton, Gene Rich, and Drs. Ernest Beerstecher, L. Joe Berry, Lorene Rogers, Eldon Sutton, and Eric Bloch. My thanks are also due Dr. Margaret Eppright, Department of Home Economics, and Donna Tullis for the release of data collected by them. Special acknowledgment is given to Dr. Th. Dobzhansky for his suggestions and assistance in preparation of this manuscript.

populations. The group of workers at our Institute has endeavored to develop such techniques, particularly to be applied for analysis of certain chemical constituents of human urine and saliva (Williams and others, '51). In the course of this work, about 1600 urine samples from some 357 individuals were analyzed. The data obtained are strictly preliminary and exploratory in nature. Not only have we restricted ourselves to samples from the white population of Texas, but even within this population chiefly male subjects of college age and upward have been studied. The available information on the age and sex differences in the excretion patterns is quite inadequate. Nevertheless, it is believed that publication of a summary of the existing data at this time is justified, particularly since such a summary will be, it is hoped, useful to other workers in this promising field. As will appear from this summary, some of the chemical constituents should be more valuable as materials for further studies than others, since the variability between individuals is much greater than the variability between repeated samples from the same individual. Similarly, some of the chemical constituents are more subject to variations with age and with sex than others.

MATERIAL AND TECHNIQUES

A majority of the persons who volunteered to furnish samples of their urine were students at the University of Texas and members of their families. The group of persons for which the data are most abundant are 272 adult males, 95% of whom were between 20 and 40 years of age, only 3 (1%) being 16 to 19 years old and 12 (4.4%) being above 40. Included in the group of adult males were 36 men who were sufferers from chronic alcoholism, although they were not drinking during and immediately preceding the days when they furnished the urine samples. A still further group of 18 adult males were patients in a mental institution. They were free from any known organic disease and all but one were diagnosed as suffering from dementia praecox. Of the women studied, 24 were between the ages of 20 and 40, and only three were over

40. Data from 58 children were included (Berry and Cain, '51a; Cain, '51). The children ranged in age from 6 weeks to 11 years.

In most cases, three to 5 morning urine samples were collected from each person. Single samples, however, were obtained from 140 individuals. The urinary excretion products are expressed using the amount of creatinine in the urine as a standard of reference. This procedure for use with morning samples was adopted as the best substitute for 24-hour samples in minimizing the effect of the rather wide variations in urine concentration. Creatinine was determined colorimetrically using sodium picrate (Bonsnes and Taussky, '45). Other urinary constituents were determined using paper chromatographic methods. The urine samples to be analyzed were placed in measured small quantities on sheets of filter paper. These sheets were stapled in the form of cylinders and placed upright in a dish containing an appropriate organic solvent-water mixture. The solvent rose by capillarity; the water, wetting and bonding with the cellulose of the filter paper, served as a stationary phase and the organic solvent as the mobile phase of the chromatographic column. The urinary constituents were deposited at characteristic positions on the paper, depending on the relative solubilities of the substances in water and the organic solvent used. The characteristic position of a substance in a particular solvent mixture, the Rf value, is defined as the ratio of the distance the substance has moved from the point of application to the distance the solvent front has moved. When two substances migrate to the same position in a single solvent, they may be separated on a two-dimensional chromatogram by using a second solvent which migrates at right angles to the first.

Most of the amino acids were determined quantitatively on two-dimensional chromatograms using phenol-salt buffer solution as the first solvent, followed by 2,6-lutidine-water as the second solvent (Berry and Cain, '51b). Histidine was determined on one-dimensional chromatograms using butanol-ethanol-2 N hydrochloric acid as the solvent and diazotized

sulfanilic acid-sodium carbonate as the developing reagent (Cain and Berry, '51). Three reagents were used routinely for developing "exploratory" one-dimensional chromatograms resolved in butanol-acetic acid-water solvent. Bromcresol green indicator was used to detect a number of acidic urinary constituents designated as BCG Rf .88 (hippuric acid), BCG Rf .76 (lactic-succinic acids), and BCG Rf .30 (citric acid). The results were recorded as area of acid per 40 μg of creatinine. Diazotized sulfanilic acid and sodium carbonate were used to reveal a group of hydroxy aromatic acids and related compounds designated as DSA Rf .60 (yellow), DSA Rf .65 (orange), DSA Rf .84 (orange), and DSA Rf .92 (rose). These substances, measured in terms of area per 100 μg of creatinine, do not necessarily represent single compounds. Ammoniacal silver nitrate was used to reveal a reducing substance in certain urine samples which was designated as AmAg reducing substance, and results were recorded as area per 40 μg of creatinine.

VARIATIONS BETWEEN INDIVIDUALS

Tables 1 and 2 show the average concentrations of certain amino acids in the urine of the individuals examined. The concentrations are expressed in milligrams of the respective substances per milligram of creatinine in the urine. The concentrations vary, of course, in the different samples from the same individual (see below), but the entries in the tables represent the arithmetical averages for all the samples taken from each individual. Table 3 reports the data on certain urinary constituents the chemical nature of which is not precisely known. Because of the lack of such knowledge, their concentrations cannot be expressed in weight units. Approximate quantification of the results is attained by planimetric measurements (in square inches) of the respective spots on the chromatograms. Since these chromatograms are made under standard conditions and with quantities of urine containing the same amount

TABLE 1

Excretion levels of urinary amino acids (expressed as milligrams of amino acid per milligram of creatinine)

CONCENTRATION	GLYCINE			HISTIDINE			TAURINE			LYSINE			β-AMINO ISOBUTYRIC ACID		
	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children
0–Trace	..	..	..	..	..	..	14	..	12	141	13	15	100	4	2
.001–.010	4	..	1	1	..	1	22	3	5	15	5	5	69	7	1
.011–.020	16	1	..	4	1	..	72	12	1	18	4	8	31	4	5
.021–.030	38	..	1	10	..	1	51	1	7	14	2	5	13	2	6
.031–.040	65	1	1	7	2	..	43	5	10	11	2	11	8	..	8
.041–.050	54	4	5	19	..	2	35	2	1	10	..	2	2	..	7
.051–.060	17	1	6	22	..	3	5	1	9	2	..	5	1	1	6
.061–.070	21	2	10	21	1	1	18	..	1	2	..	3	1	..	5
.071–.080	23	3	7	25	2	1	5	..	2	4	..	2	1	..	4
.081–.090	9	2	3	23	2	3	1	..	3	1	..	..	..	..	1
.091–.100	9	..	4	16	2	3	3	1	1	5	..	..	3	..	1
.101–.110	3	2	3	13	3	2	..	..	1	..	..	..	..	..	2
.111–.120	2	4	1	13	4	1	..	..	2	..	..	..	2	..	..
.121–.130	4	1	1	12	..	5	2	..	1	3	..	..	2	..	1
.131–.140	2	..	2	13	1	..	..	..	..	..	..	1	2	..	1
.141–.150	..	1	1	9	..	1	..	..	..	..	1	..	..	..	..
.151–.160	..	..	..	5	1	5	..	..	..	..	..	..	..	..	..
.161–.170	..	..	1	9	..	4	..	..	..	..	..	..	..	..	..
.171–.180	..	..	1	3	1	1	..	..	..	..	..	..	..	..	1
.181–.190	1	1	..	5	..	4	1	..	..	1	..	..	..	..	1
.191–.200	2	..	..	4	..	1	..	..	..	1	..	..	..	..	..
.21 –.30	2	2	3	13	1	12	..	..	..	1	..	..	2	..	2
.31 –.40	..	..	4	..	..	7	..	..	..		..	..	..	..	..
.41 –.50	..	..	1		..	..	..	..	..	..	..	..	..	..	..
.51 –.60	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
Mean	0.053	0.100	0.139	0.100	0.104	0.148	0.030	0.026	0.037	0.017	0.012	0.027	0.014	0.010	0.061
σ	.032	.063	.128	.052	.053	.104	.023	.020	.032	.035	.031	.027	.033	.014	.052
Number	272	25	57	247	21	58	272	25	56	229	27	57	237	18	54

TABLE 2

Excretion levels of urinary amino acids (expressed as milligrams of amino acid per milligram of creatinine)

CONCENTRATION	SERINE			ALANINE			GLUTAMINE			LEUCINE			ASPARTIC ACID		
	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children
0 or Trace	19	1	5	5	..	4	6	..	6	141	4	19	166	7	29
.001–.005	9	..	..	14	3	.	6	2	.	18	7	5	3	1	9
.006–.010	10	..	1	48	2	2	41	3	1	23	5	8	2	1	6
.011–.015	43	2	1	86	6	.	58	3	6	21	2	5	..	..	7
.016–.020	47	..	1	62	5	9	59	4	2	13	2	7	..	..	3
.021–.025	41	3	1	27	3	6	41	5	5	10	1	2	..	..	..
.026–.030	15	2	2	12	3	3	22	3	8	1		3	1	..	..
.031–.035	26	1	1	8	1	4	12	3	3	1	1	3	..	..	..
.036–.040	18	1	1	1		2	4	1	4	..	..	3	..	..	..
.041–.045	8	1	3	2	1	3	1	..	4	2	.	..	..	..	..
.046–.050	19	..	6	..	.	8	2	..	4	..	.	..	..	..	..
.051–.055	2	1	3	..	.	2	..	..	3	..	..	.	..	..	..
.056–.060	2	1	3	1		3	1	1	2	..	.	.	..	..	..
.061–.065	7	..	6	1	..	3	2	.	3	..	..	..	..	..	..
.066–.070	..	1	8	1	..	2	.	..	1	..	..	..	..	..	..
.071–.075	4	1	4	.	.	1	.	..	2	..	..	..	..	..	..
.076–.080	..	2	2	..	..	1	..	..	1	..	..	..	..	..	..
.081–.085	..	1	1	..	..	..	..	..	1	..	.	..	..	..	..
.086–.090	1	.	..	..	..	..	..	..	..	.	..	..	..	..	..
.091–.095	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..
.096–.100	..	..	..	..	..	2	1	..	1		.	..	..	..	..
.101–.110	..	..	3	..	..	..	..	..	..	..	..	..	..	..	..
.111–.120	1	..	1	.	1	1	..	..	..	..	..	..	..	..	..
.121–.130	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
.131–.140	..	..	1	..	..	..	..	..	..	..	..	.	..	..	..
.141–.150	..	..	2	.	..	..	..	..	..	..	..	..	..	..	..
Mean	0.026	0.047	0.059	0.016	0.021	0.037	0.019	0.022	0.035	.005	0.008	0.014	0.0003	0.001	0.004
σ	.018	.026	.035	.009	.024	.025	.011	.012	.023	.008	.008	.012	.0024	.002	.005
Number	274	18	57	268	25	56	256	25	57	239	22	55	172	9	54

TABLE 2 *(continued)*

Excretion levels of urinary amino acids (expressed as milligrams of amino acid per milligram of creatinine)

CONCENTRATION	GLUTAMIC ACID			NO. 16 (ETHANOLAMINE) (AS ALANINE UNITS)			THREONINE			TYROSINE			VALINE		
	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children
0 or Trace	82	7	9	152	5	2	101	3	23	128	3	9	108	5	10
.001–.005	48	7	7	28	8	9		6		8	1	1	33	8	5
.006–.010	76	5	12	30	1	4	26	1	2	16		2	46	7	6
.011–.015	16	1	3	7			27	6	1	9	1	8	23	1	11
.016–.020	3	1	4	2			6	3	4	18		2	12	1	6
.021–.025	3	1	4				5	1	3	21		4			7
.026–.030	2	1	2						1	2		3	1		3
.031–.035		1	1						2	2		1			2
.036–.040			1				1		2	4		3			4
.041–.045			2						2	2					
.046–.050										4		2			1
.051–.055		1	1						1				1		
.056–.060			2				1		1						
.061–.065										1		1			
.066–.070			2						2			1			
.071–.075							1								
.076–.080															
.081–.085												1			
.086–.090															
.091–.095															
.096–.100							1		1						
.101–.110															
.111–.120			1												
.121–.130			2												
.131–.140															
.141–.150			1												
Mean	0.005	0.005	0.027	0.002	0.002	0.004	0.007	0.009	0.017	0.008	0.003	0.020	0.005	0.005	0.015
σ	.005	.014	.041	.003	.002	.002	.012	.007	.024	.012	.005	.021	.006	.004	.012
Number	230	25	54	219	14	15	169	20	45	215	5	38	223	22	55

TABLE 3

Levels of urinary diazonium coupling compounds (DSA), weak acids (BCG), and ammoniacal silver nitrate reducting substance (AmAg. Red.)

	DSA Rf .84			DSA Rf .65			DSA Rf .92			DSA Rf .60			BCG Rf .30			BCG Rf .76			BCG Rf .88			AmAg Red.
	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men	Women	Children	Men
0 or Trace	18	..	6	50	3	8	20	..	2	194	14	28	9	3	6	109	8	11	6	..	6	154
.01– .05	6	..	1	15	..	5	21	2	2	11	..	6	3	..	1	18	..	1	16	..	2	1
.06– .10	16	..	2	44	2	7	58	1	6	11	2	2	5	1	6	29	..	7	48	3	2	2
.11– .15	23	..	4	37	3	10	51	7	7	5	2	..	5	1	4	10	3	7	56	3	4	1
.16– .20	28	3	6	32	4	3	41	5	11	4	1	..	4	1	2	4	..	8	38	6	11	2
.21– .25	23	3	9	21	3	2	14	2	3		..	..	4	2	1	2	..	12	29	2	13	6
.26– .30	18	3	1	11	3	..	3	1	3	..	..	..	3	..	4	2	..	8	18	1	7	2
.31– .35	17	1	2	5	1	..	2	1	..	..	..	..	3	..	4	..	..	4	8	..	5	2
.36– .40	11	2	1	4	..	..	3	..	1	..	..	..	..	1	1	1	..	..	7	2	8	2
.41– .45	15	..	3	4	..	..	1	..	..	..	..	..	1	..	1	1	..	..	3	2	2	1
.46– .50	13	2	1	..	..	..	..	..	..	..	..	..	1	..	2	..	..	..	5	..	..	..
.51– .55	5	..	..	..	..	..	..	..	..	.	..	..	1	..	1	2	1	..	1	..	..	..
.56– .60	8	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	..	..	1	..	..	..
.61– .65	9	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	1	1	1	..	..
.66– .70	7	2	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	2	..	..	..
.71– .75	3	1	..	..	..	..	.	.	.	.	.	..	..	..	..	.	.	..	..	..	..	..
.76– .80	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
.81– .85	2	1	..	.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	.	..
.86– .90	..	..	..	.	..	..	..	..	..	..	..	..	..	..	..	1	.	.	.	..	..	..
.91– .95	1	..	..	..	..	..	.	..	..	.	.	.	..	..	..		.	.	..	..	..	..
.95–1.00	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Mean	.28	.39	.19	.13	.11	.09	.12	.16	.15	.01	.04	.01	.16	.14	.21	.05	.08	.17	.19	.23	.18	.03
σ	.21	.22	.13	.12	.10	.07	.07	.09	.08	.03	.05	.02	.17	.12	.17	.11	.15	.12	.13	.15	.10	.08
Number	225	19	36	223	19	35	214	19	35	225	19	36	39	9	35	183	12	59	242	20	59	173

of creatinine, the concentrations of these substances in different urine samples may validly be compared.

It can be seen at a glance that individuals vary greatly in the composition of the urine which they excrete. Only glycine and histidine are present in measurable amounts in every sample studied; yet in some individuals the concentrations of these substances are 40 to 60 times greater than in others. All other substances mentioned in the tables were either absent, or present in concentrations which could not be detected with the methods used, in at least some of the individuals examined. For example, lysine was not detected in 169 individuals. On the other hand, one individual, a college student, produced more than 0.21 mg of lysine per milligram of creatinine in his urine. It may be noted that this man was perfectly "normal," in the sense that he showed no obvious disease or abnormality in appearance or behavior. Glycine, glutamine,[2] alanine, and serine are the most important constituents in nearly all urine samples examined, in the sense that these amino acids give the most conspicuous spots on chromatograms made with phenol-lutidine and developed with ninhydrin. Yet, in some individuals one or more of these "major" spots was absent, while spots produced by some other amino acids were very prominent. (Visual prominence of spots produced by different substances is, of course, not always proportional to the concentration of the latter. Thus, leucine begins to be detectable at concentrations much higher than, for example, alanine.) At any rate, so great is the variation that chromatograms can be the basis for distinguishing between individuals.

There is some evidence in the data that the concentration of certain substances in the urine changes with age and is also different in the two sexes. As shown in the tables, children have, on the average, significantly more glycine, glutamic acid,

[2] In previous publications (Berry, '51; Dent, '48) this substance has been referred to as citrulline, ninhydrin spot no. 7, or citrulline/glutamine/β-alanine. Evidence indicates that in a majority of urine samples analyzed here glutamine is the principle component of ninhydrin spot no. 7 rather than citrulline. Since the identity of the substance was uncertain, the results are expressed as milligrams of alanine per milligram of creatinine.

and BCG Rf .76 than do adult men. Children excrete probably also more lysine, serine, β-amino isobutyric acid, valine, alanine and glutamine than do adult men. The number of samples from adult women is too small in our material to yield significant differences, but taken as a whole the data suggest that the urinary excretion patterns of children deviate less from those

TABLE 4a

Number of children of different ages excreting different levels of glutamic acid

CONC. OF GLUTAMIC / AGE (yrs.)	0.5	1	2	3	4	5	6	7	8	9	10	11	Total
0 or trace	..	..	..	..	..	..	..	2	..	5	2	..	9
.001–.010	..	..	1	2	1	1	1	2	5	2	1	3	19
.011–.020	..	..	..	..	1	..	2	1	..	..	2	1	7
.021–.030	..	1	1	2	1	..	..	..	1	..	..	..	6
.031–.040	..	..	..	1	..	..	..	..	1	..	..	..	2
.041–.050	..	..	1	..	1	.	..	..	..	..	..	..	2
.051–.060	..	1	..	..	..	1	1	..	..	..	..	..	3
.061–.070	..	..	..	2	..	..	..	..	..	..	..	..	2
.071–.100													
.101–.150	2	..	1	..	..	.	..	..	..	..	..	..	3
.151–.200	..	..	..	..	..	..	..	..	..	..	..	..	..
.201–.300	..	..	1	..	..	.	..	..	..	..	..	..	1
Total	2	2	5	7	4	2	4	5	7	7	5	4	54

TABLE 4b

Number of children of different ages excreting different levels of glycine

CONC. OF GLYCINE / AGE (yrs.)	0.5	1	2	3	4	5	6	7	8	9	10	11	Total
0 or trace	..	..	..	..	..	..	..	..	..	..	..	..	..
.001–.020	..	..	1	..	..	..	..	..	..	..	..	..	1
.021–.040	..	1	..	..	..	..	1	..	1	1	..	..	4
.041–.060	1	..	1	1	1	.	1	1	2	3	..	..	11
.061–.080	..	..	..	1	1	.	..	1	3	3	5	2	16
.081–.100	..	..	..	1	..	1	..	2	..	1	..	1	6
.101–.15	1	..	1	1	1	1	..	2	..	..	1	..	8
.16 –.25	..	..	1	..	..	1	1	..	..	..	..	..	3
.26 –.35	..	..	1	1	..	..		..	..	..	..	..	2
.36 –.50	..	..	1	2	..	.	1	..	1	..	..	..	5
.50 or above	..	1	..	..	..	..	..	..	.	..	..	..	1
Total	2	2	6	7	3	3	4	6	7	8	6	3	57

of adult women than from adult men. Nor can we be sure that boys differ appreciably in excretion patterns from girls; the most suggestive difference of that kind indicated by the data is that boys tend to excrete less glycine than do girls, which is parallel to the difference between the adult men and women.

Correlation between age and excretion of glycine and glutamic acid in children is shown in tables 4a and b. The higher concentrations of these amino acids are excreted in general by the younger children, though the same children may not excrete large quantities of both amino acids.

The variation curves indicated by the data in tables 1–3 are all more or less asymmetrical. For many substances the most frequent class is zero concentration. The prevalence of zero variants does not necessarily mean that the respective substances are wholly absent in the urine of most subjects, but only that their concentrations are too small to be detected by the methods used. Certainly the chromatograms made with quantities of urine containing 40 μg of creatinine show fewer discernible spots than those made with samples containing 80 μg of creatinine. Nevertheless, it is probably significant that even for the substances which are detected in all the samples the variation curves are skewed towards the left. It is possible that expressing the variations in terms of logarithms of the relative concentrations might be a better method of treating the data, but more observations are needed to settle this point. It may also be noted that the observed distributions for glycine, histidine, lysine, β-amino isobutyric acid, serine, tyrosine, glutamic acid, DSA Rf .84, and BCG Rf .76 strongly suggest bimodality or even multimodality. The available observations are insufficient also to decide the validity of this suggestion.

VARIATIONS BETWEEN SAMPLES FROM THE SAME INDIVIDUAL

As stated above, the data in tables 1–3 give average concentrations of various substances in the urine of certain indi-

viduals. More than a single sample collected on mornings of successive days or at still longer intervals was studied for a majority of individuals. Since the donors were on self-selected diets which doubtless varied from day to day, the observations give some basis for judging the degree to which the urinary patterns are characteristic for the individual donors. A general impression, based on several years' experience of working in this field, may be stated as follows. The chromatograms obtained from different samples from the same donor are in general much more similar than chromatograms of urine from different donors. Quite often the chromatograms from the repeated samples are almost identical, which seldom or never happens with samples from different individuals (identical twins are the possible exceptions: see Berry, Cain and Rogers, '51).

Probably the most efficient way of analyzing the variations between samples and those between individuals is to compare the variances in the respective distributions. This can be done with the aid of simple formulae devised by Professor H. Levene of Columbia University and used by Dobzhansky and Spassky ('53) for their materials. The variance of individual means is:

$$\Sigma\ (\bar{x}_1 - \bar{x})^2 / (K - 1)$$

The variance between samples from the same individual may be computed from the formula:

$$[\Sigma\Sigma\ (x_1 - \bar{x}_1)^2 / r\ (r - 1)] / K$$

In these formulae, K is the number of individuals studied; x_1, the concentration of a given substance in a single sample; x_1, the average concentration in samples from a given individual; $\bar{x}$, average concentration in all individuals; and r, the number of samples studied in each individual concerned.

The variances between samples and between individuals are summarized in table 5. The rightmost column shows the ratios obtained by dividing the variances between individuals by those between samples. These ratios furnish a measure of the extent to which the concentrations of various substances differ significantly in the excretion patterns of the various indi-

viduals studied. All the data in table 5 are based exclusively on samples from adult men.

One of the highest variance ratios, 29.9, is observed for β-amino isobutyric acid. This is the substance which Harris ('53) found, with the aid of the methods used by him, to be present in

TABLE 5

Summary of variances

COMPOUND	OBSERVED VARIANCE (Between individuals)	SAMPLING VARIANCE (Within individuals)	RATIO OF OBSERVED TO SAMPLING VARIANCE
Glycine	1055.45	146.79	7.2
Serine	318.04	72.91	4.35
Histidine	2675.6	608.07	4.4
Taurine	534.44	121.02	4.4
Alanine	81.32	18.62	4.35
Glutamine	121.07	39.15	3.1
Glutamic acid	25.10	11.52	2.2
Aspartic acid	5.71	0.18	31.8
Lysine	1244.81	81.31	15.3
Threonine	137.35	6.87	20.0
Valine	39.32	12.84	3.05
Leucine	56.85	16.28	3.5
β-amino isobutyric acid	1096.38	36.69	29.9
Ethanolamine	10.54	4.45	2.4
Tyrosine	142.90	27.18	5.25
DSA Rf .60	10.97	4.3	2.55
DSA Rf .65	100.0	11.76	8.5
DSA Rf .84	433.63	88.11	4.9
DSA Rf .92	53.28	11.22	4.7
BCG Rf .30	274.84	10.86	25.4
BCG Rf .76	129.84	16.39	7.9
BCG Rf .88	162.41	34.19	4.8
AmAg reducing substance	64.87	12.19	5.3

the urines of some 9% of the inhabitants of London which he studied, and absent in the remainder. Harris infers, on the basis of the pedigrees which he has examined, that the excretion of a large concentration of this substance is due to homozygosity for a recessive gene. The minimum amounts of β-amino isobutyric acid detected by Harris are about 0.070 mg per milligram of urinary creatinine. In the material shown in

table 1, 26 individuals excreted concentrations as great or greater than this, and 282 individuals had lower concentrations. This corresponds to about 8.4% homozygous individuals, which is a frequency not significantly different from that recorded by Harris.

Other substances which show the greatest variances between individuals relative to between samples from the same individual are BCG Rf .30, aspartic acid, threonine, lysine, DSA Rf .65, BCG Rf .76, and glycine. BCG Rf .30 is in all probability citric acid, and BCG Rf .76 is probably lactic acid. The nature of the other unidentified substance, DSA Rf .65, is more problematical, but preliminary evidence indicates that it may be a substituted phenol or hydroxy aromatic acid.

Variance ratios below 4 are probably not significant. Concerning substances for which the variance ratios are relatively small, it should be noted that the prevalence of the zero samples may be a disturbing factor. Thus, leucine shows a ratio of only 3.5. However, this substance is present only in trace amounts in most of the samples studied. Some individuals excrete consistently large amounts of leucine day after day. The same is true also for BCG Rf .88, which is probably hippuric acid or a related compound; although it is variable from sample to sample, some individuals are quite consistent producers, and others non-producers, of this substance.

DISCUSSION

The data reported in this article demonstrate clearly that different "normal" human individuals have different urinary excretion patterns. Some people excrete considerable amounts of certain substances which are present in much smaller or even undetectable concentrations in the urine of other persons. The differences are chiefly quantitative, but they are often so large that certain individuals are clearly "marked" by their urinary constituents.

The interpretation of these data can at present be only tentative. At once the question arises: are some or most of the differences recorded genotypically conditioned? The data

available show only that the differences between individuals are very often greater than those between samples from the same individual. Since our material came chiefly from volunteers who led their "normal" lives and were on self-selected diets, it is certain that these donors were not living on uniform diets or in uniform environments. That the presence of certain substances in the urine depends on the diet is, of course, too well known to need emphasis (Datta and Harris, '51). A part of the variance between individuals is, thus, environmental rather than genetic.

Special studies are needed to find out the roles of heredity and environment in the production of the metabolic differences recorded. In particular, data on members of families (parents and their children) are necessary. The experience with the type of work described above gives numerous indications that at least some of the features of the urinary excretion patterns are not environmental. Certain individuals excreted day after day very large, or very small, amounts of some substances which were present in quite different concentrations in other persons who had visibly the same diets and apparently similar daily routines. Conversely, the same individuals continued to show certain conspicuous traits, despite having had unusual meals or engaged in diverse forms of activity on different days when samples were taken. The urinary excretion pattern of one adult woman has remained constant over a period of 5 years. The excretion patterns of small babies whose diets are made up almost wholly of milk show that they exhibit distinctive and consistent differences. In an earlier study by Thompson and Kirby ('49) using microbiological methods, the patterns of amino acid excretion were found to be essentially unchanged with a radical change in diet, from self-selected diets to U.S. Army K rations. The similarity of patterns of identical twins has been mentioned. Urinary excretion patterns of highly inbred strains of rats (Reed, '51) kept for several months on a uniform diet indicated the existence of striking strain differences, especially involving the excretion of lysine, taurine, and β-amino isobutyric acid, as well as highly

individual differences in the animals within a strain. Taken singly, none of these observations proves conclusively the hereditary basis of any of the metabolic traits involved, but the evidence as a whole is convincing at least to those having experience in this type of work. To make the proof convincing to others more data are needed.

SUMMARY

Chromatographic analysis has been made of 1600 urine samples from 357 white individuals resident in the state of Texas (272 adult men, 27 adult women, and 58 children). The donors were on self-selected diets, and, with the exception of 18 men who were patients in a mental hospital, were engaged in their normal occupations. Most individuals furnished three or more urine samples taken on the mornings usually of successive days.

The concentrations of several urinary constituents were determined and expressed in relation to the amount of creatinine present in the urine samples (tables 1–3). These concentrations vary greatly in different individuals, so much so that the chromatograms of two individuals in general are easily distinguished. Variations from day to day also occur, but they are in general much smaller than those between individuals. The greatest ratios of the variances between individuals and those between samples from one individual occur for aspartic acid, β-amino isobutyric acid, threonine, lysine, and certain substances the precise chemical nature of which is at present unknown (table 5).

Although the concentrations of the urinary constituents are doubtless somewhat influenced by dietary and other factors, the evidence indicates that a considerable part of the observed variance between individuals is genotypically conditioned.

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A HANDBOOK OF THE MEASUREMENT AND INTERPRETATION OF HEIGHT AND WEIGHT IN THE GROWING CHILD.— By Wilton Marion Krogman. Monographs of the Society for Research in Child Development. Vol. 18, no. 3. Serial no. 48, ix + 68 pp., Child Development Publications, Evanston. 1950.

This 68 page handbook, completed in 1949, is a short summary and description, a kind of commentary on pages 70–301 of the author's earlier "Growth of Man." Simply written, and with a minimum of criticism, it reviews the subject. It tells how to measure, what errors are likely, and how to put height and weight together, in the form of an index, on a growth chart, or on a Wetzel Grid. There is also a short bibliography, and some theoretical material.

Because of its simplicity, and the lack of excessive criticism that so often leaves the student wondering whether anything is good, this handbook is suitable for class use. However the lack of a critical approach may disturb the research worker. After all, the Wetzel Grid contains some mighty weak assumptions that Wetzel does not discuss, but Dössing did. And the indices of body build; just exactly what do they tell once they have been computed? But Dr. Krogman has sought to be constructive, to stress the doughnut and not the hole, and the "Handbook" reflects this attitude.

SUBCUTANEOUS FAT AND AGE CHANGES IN BODY BUILD AND BODY FORM IN WOMEN [1]

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WITH THE ASSISTANCE OF
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ONE FIGURE

"It cannot be too strongly emphasized that the contours of the body depend as much upon the total amount of subcutaneous fat and upon the shape of the bone and muscle mass, as upon the distribution of the subcutaneous fat." (Edwards, '51a.)

INTRODUCTION

Body build and body form are two aspects of a broader concept of "constitution." Unfortunately, no general agreement exists on the definition or usage of this term in human biology (Kaplan, '50), although most authors employ it with some reference to body form or structure. It is also used loosely to designate an individual's genetic endowment, as expressed both in his physique and in his functions or behavior. Jankowsky ('30), not without reason, speaks of partial constitutions, meaning that the body build is one expression of constitution, but not the only one.

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Even with reference to human physique, one cannot adequately characterize "constitution" by a single formula or by a simple numerical symbolism which deceptively appears to be exact and comprehensive. One important aspect of physical constitution is the individual variability of the skeletal frame, especially the width of the body in relation to its length or height — a ratio which remains fairly constant in adults from about 20 to 60 years of age. Body build, determined by the skeletal frame, is thought to be reflected also in some non-skeletal parts (Weidenreich, '27; Škerlj, '48).

A second aspect of human somatic variations is the over- or under-development of the soft tissues, characterized as hyper-, normo-, or hypoplasia (H-n-h), which is evaluated, in the present study, by inspection. An important limitation of this method is that it is difficult to discriminate adipose from muscle tissue.

A third area of measurable somatic variations is the distribution of soft tissues which are close to the body surface (skin and subcutaneous fat). These layers can be measured either from roentgenograms or by skinfold calipers, and results by both methods agree closely, according to Baker (unpublished study, Forsyth Dental Infirmary, Boston). The x-ray method, applied to several body regions by Reynolds ('51), has yielded data on age trends in children, but information available so far does not permit us to examine age trends in the distribution of subcutaneous tissues in adult women. This problem was examined by Edwards ('51), using skinfold calipers. At present, we know next to nothing about the relationship of subcutaneous fat to total body fat, not to mention age changes in this pattern.

A 4th method of evaluating the "anatomy of the living man" has progressed considerably within the last decade, and is based on the determination of the density and water content of the body (Brožek, '53a; Keys and Brožek, '53). Data on the sex and age differences found in the specific gravity of the adult have been reported briefly by Brožek et al. ('53).

The present study is focussed on the second and third aspects of constitutional variations in women: the development of soft tissues and the distribution of fat, with reference to their changes with age. At present, most research on human aging is being carried out cross-sectionally, using samples of different individuals at different age levels. Longitudinal studies, which could prove conclusively the nature of some of these age changes, require studying the same individuals throughout adult life. Such an approach involves almost insurmountable technical, human and administrative difficulties. With some reservations, then, the data which follow are presented as indications of authentic age changes, even though a few differences may have resulted from sampling individuals of different ages at the time of the study.

SUBJECTS AND METHODS

A series of 84 women, unselected with reference to body weight, volunteered for this study, which was carried on at the Laboratory of Physiological Hygiene, University of Minnesota, in the summer of 1952. At that time, the personnel of the Laboratory determined the specific gravity of the subjects by underwater weighing at 35–36°C., and measured the thickness of subcutaneous fat by skinfold calipers. The caliper points exerted an opening pressure of 5.4 gm/mm^2, and the pressure increased negligibly as the thickness of the skinfold increased. The skinfolds were measured with the subjects in the nude. Each subject, dressed in a bathing suit, was also examined by Doctor Škerlj. Stature and weight were determined, and the body form evaluated by direct inspection. It was not feasible to take nude body-build photographs.

The 10 sites chosen for the measurement of skinfolds were selected mainly on the same *a priori* grounds as Brožek and Keys ('51) stated for men: "The following conditions were to be satisfied: (1) representation of regions known to show large variations in subcutaneous fat (abdomen, chest), (2) representation of the extremities (arm and thigh measurements), and (3) ease of location."

The skinfold sites, except for the chin, were all measured on the right side of the body. The following sites were included:

1. *Chin* under the mandible, with the peak of the skinfold extending from chin to neck.
2. *Back* under the scapula.
3. *Chest* at the axillary border of the pectoralis major muscle. This location was somewhat higher in women than in the study of men.
4. *Side* at the lateral part of the thorax over the lower ribs, midway between the axilla and the iliac crest.
5. *Waist,* between the ribs and iliac crest.
6. *Abdomen,* to the right of the umbilicus.
7. *Arm* halfway between the shoulder and elbow over the triceps muscle.
8. *Thigh* halfway down, over the rectus femoris muscle.
9. *Knee* just above the patella.
10. *Calf* on the back of the gastrocnemius muscle, at the level of the maximal circumference. This fold was often difficult to measure, even with a maximal effort to relax the muscle.

The folds on the lower limb were measured with the subject seated and the limb extended but relaxed. The 10 skinfolds were measured in succession three times, thus yielding three independent readings for each site. These readings were averaged. For each subject, the 10 thicknesses were summed and a grand mean calculated. This mean is an estimate of the true mean skinfold thickness for the entire body surface.

A skinfold thickness is a composite of two layers, each including skin and subcutaneous adipose tissue. Edwards ('50) found that the mean skin thickness is about 1 mm. We obtain the thickness of a single layer of subcutaneous adipose tissue by subtracting this value from one-half of the skinfold.

For the grand mean thickness of skinfolds, used in the calculations of the weight of the subcutaneous fat, a larger correction (3 mm) was subtracted in an effort to compensate not only for skin thickness, but for the fact that our average

skinfold value was higher than the true average for the body as a whole. The volume of an individual's subcutaneous adipose tissue was obtained by multiplying the grand mean thickness of the adipose layer by the surface area of the body, obtained from the nomogram of DuBois ('36). The weight of the tissue was calculated by multiplying the volume by 0.94, the approximate density of adipose tissue. Weight of the adipose tissue, multiplied by a factor of 0.42 (Mitchell et al., '45), yielded the weight of subcutaneous fat (ether extract). Total body fat was estimated from specific gravity by the method of Rathbun and Pace ('45) and the weight of inner fat ("Total"-"Subcutaneous") was calculated.

At our present state of anthropometric skill, quantitative data cannot fully replace morphological observations in the evaluation of human body form. The skinfold caliper, for example, can only be used where a fold can readily be lifted. Other body regions may be studied through roentgenograms, but, in the present study, this approach was not feasible. Breasts, buttocks and trochanteric fat pads were therefore evaluated visually.

The inspection of the living body also has the advantage that the subject can be considered from all aspects and in motion. Frequently pressed for time, however, even a trained observer can make mistakes. From this viewpoint, body typing on standardized photographs has its advantage — time. But, as such photographs show the body only in two or three aspects in an erect position, it is not always possible to evaluate the tissue relationships (skeletal frame, muscles, and adiposity) with the desired certainty.

Škerlj's ('30, '38, '48, '50) classification of variations in female body form stems from the typology of Bauer ('23). These variations reflect primarily the localization of subcutaneous fat and, less directly, the development of underlying tissues. In its revised form, this classification is a system of vectors. These vectors are continuous variables, largely independent of each other, but by no means quantitative nor precise measurements. The extremes of the vectors can be

spoken of as "types," but these types are by no means static concepts.

A vector, then, is a variation of body form characterized by a dominant localization of massive body structures, particularly adipose tissue. Most of the vectors can be thought of as extending from an origin of coordinates which is harmoniously moderate in fatness throughout the body (N, or normal). The N condition is typical of the mature female body.

The vector concept resembles that of component dominance in somatotyping (Sheldon, Stevens and Tucker, '40), where, for example, an individual may be rated as a "dominant endomorph." The degree of expression of a given vector might be indicated numerically. Descriptive standards and visual norms would improve the precision of the method. At present, however, the treatment is purely qualitative. Only the presence or absence of a well-defined vector, not its magnitude, is noted.

The first vector is a continuum of variations in body form from a lean (L) pole, with a harmonious deficiency of fat, through a normal (N), or harmonious and moderate distribution, to an abundant but still harmonious obesity. This obesity is reminiscent of the paintings of Rubens, and is therefore referred to as the adipose, or Rubens extreme (Type R. See fig. 1). In the present data, lean women have been included in the "normal" category rather than tabulated separately.

The other vectors of body form diverge away from the "normal" toward more or less localized thickenings of the panniculus adiposus in specific body regions. The second vector continuum varies from a superior (S) to an inferior (I) extreme. At the superior end of the scale, obesity occurs above the waist. At the inferior end, adipose tissue is localized in the hips and lower extremities.

A third vector contrasts a central with a peripheral distribution of fat. At the central extreme, obesity is localized in the trunk rather than in the limbs, so that the form of the body can be called truncic (Tr). This central distribution

was formerly called "juvenile" (J), because of its prevalence in preadolescent obesity. But since it is also common in middle age, it seems advisable to refer to the truncic extreme or type instead. Angel ('49) has introduced this concept into the literature in English in his descriptions of a very prevalent distribution of fat in obese women. At the peripheral

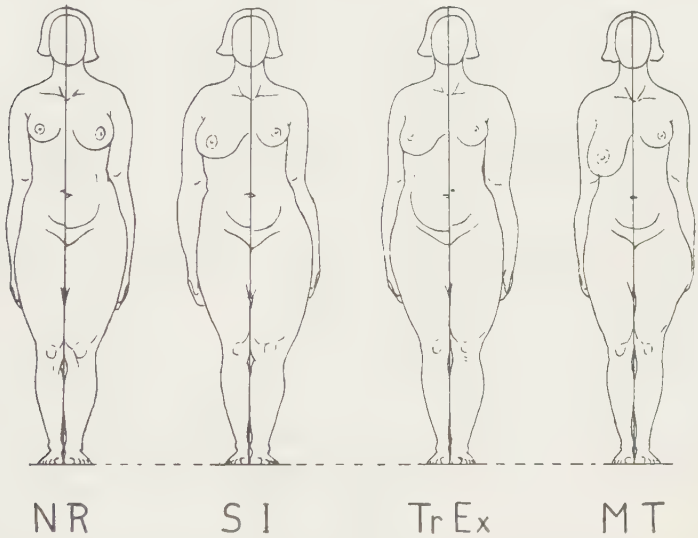

Fig. 1 Pictorial representation of the extremes (types) of body form with reference to the amount and distribution of soft tissue. (N: normal. R: Rubens. S: superior. I: inferior. Tr: truncic. Ex: extremital. M: mammary. T: trochanteric.)

extreme of this continuum, fat is localized in the limbs but not in the trunk, so that the body form is rated as extremital (Ex).

Additional vectors can be extended from the normal form in the direction of fat padding in three more localized regions. All of these vectors are apt to be more apparent in women than in men. One refers to large fat deposits in the breasts (mammary, or M vector). The second vector represents the development of large fat pads over the greater trochanters of the femora (trochanteric, or T vector). Thirdly,

fatness may be localized in the buttocks, a condition described by the pseudosteatopygous (Pst) vector. A body form in which the Pst vector is strongly evident in white women is actually more reminiscent of a Paleolithic female statuette than of the steatopygia found in some Hottentot women.

It is of considerable interest that Howells ('52) found quantitative factors of male physique which are somewhat similar to the qualitative factors of body form termed L-N-R, S-I, and Tr-Ex. Howells' first factor expresses body mass, opposing endomorphy directly to ectomorphy, and reflects the amount of padding between the skin and bones. The second factor opposes top-heaviness to bottom-heaviness. The third factor opposes trunk (and face) development to limb development. Howells' paper provides a valuable confirmation of the ability of a trained observer to perceive fundamental variations in body form by inspection.

Howells' male factors differ from the vectors of Škerlj in that the vectors were conceived to be more direct expressions of the distribution and quantity of subcutaneous fat: whereas Howells' factors reflect bone, muscle and other lean tissues as well as fat. This difference chiefly derives from what Škerlj ('30) called the "physiological obesity of the female body." Edwards ('51), using skinfold calipers, obtained 640 mm as the total of 53 skinfold thicknesses for young women of average weight for height, and 412 for men, yielding a ratio of 1.55 (not 1.75, as indicated by the author). Calculations of total body fat from specific gravity suggest still larger sex differences in this respect (Brožek et al., '53; and Chen, Carlson and Brožek, '53).

Škerlj ('38), has not only developed criteria in terms of which female body forms can be described, but also examined measurements (especially circumferences) by which these tendencies can be sorted out metrically. Even the Mammary and Trochanteric vectors, which are typically feminine variations, can be revealed by these metrical techniques. Such measurements are important initial steps toward the characterization of the vectors of body form. In the future, a

factor analysis of women's body measurements may well confirm the statistical validity of some of them, and also enable us to evaluate them quantitatively.

RESULTS

The 84 women measured in this study ranged from 18 to 67 years of age. They were divided into three age groups as seen in table 1. The mean statures, weights, and weights relative to the Medico-Actuarial Investigation standards of 1912 are also provided in this table.

The women studied in this series averaged close to the female means for stature in the United States, but were light

TABLE 1

Age, stature and weight of the three groups

GROUP	N	RANGE	AGE		HEIGHT *cm*		WEIGHT *kg*		RELATIVE WEIGHT	
			M		*M*		*M*		*M*	
A	31	18–30	24.0	2.6	162.6	6.2	54.69	6.8	94.13	9.14
B	25	31–45	39.8	4.4	163.2	6.5	61.26	6.8	96.95	9.44
C	28	46–67	55.4	5.3	160.6	6.2	61.60	11.0	95.18	15.06

relative to the 1912 weight standards, applied to nude weight with no "correction" for the absence of shoes and clothing. Another morphological characteristic of this sample is the relationship of breadth to length of the skeletal frame, as determined by visual inspection. This "constitutional" continuum ranges from a broad or "eurysomatic" (E) extreme through three intermediate degrees to a narrow or leptosomatic (L) extreme. Table 2 shows the distribution of skeletal frames in the three age groups of women in this sample.

The three age groups appear to differ in their skeletal frames. We do not know anything certain about age changes in this respect in the general population. In this series, the youngest group has a preponderance of eurysomatic frames, while the oldest shows a contrary trend toward more leptosomatic extremes. Perhaps the youngest group has been more

physically active than the older one, and this activity may have stimulated skeletal development toward the E extreme. The samples are too small, however, to permit definite conclusions on these matters, and no metrical data are available on skeletal breadths.

The development of soft tissues in the three age groups of women was evaluated by inspection. The continuum of this

TABLE 2

Skeletal frames (Eurysomatic-Leptosomatic body form)
Percentage frequencies for the three age groups

GROUP	N	E	EL	ELLE	LE	L
A	27	44.5	18.5	22.2	14.8	0.0
B	25	28.0	28.0	24.0	16.0	4.0
C	27	22.2	33.2	14.8	18.6	11.1

TABLE 3

Soft tissue development

GROUP	N	DEGREE OF HYPER-HYPOPLASIA				
		H	Hn	n	nh	h
A	28	3.6	3.6	57.2	10.7	25.0
B	25	16.0	32.0	32.0	16.0	4.0
C	27	14.8	37.1	25.9	11.1	11.1

variable ranges in 5 steps from the hyperplastic (H) extreme through normoplastic (n) to hypoplastic (h). The results are presented in table 3.

With increasing age, hyperplastic ratings increase while the normoplastic and hypoplastic individuals become rarer. A partial reversal of this tendency is seen, however, in the oldest group. It is not clear whether sampling, aging or other factors account for this.

A fully satisfactory estimate of the amount of subcutaneous fat in the body is not possible at present. Our averages are based on skinfold sites which are probably more adipose than the body surface as a whole. Even though the absolute

amounts calculated here are probably too high, the trends shown in table 4 indicate a slight tendency toward an increase in the contribution of subcutaneous adipose tissue to total body weight with age in women.

On most, but not all, of the women in this series, both skinfold measurements and underwater weights were determined. These two techniques together allow us to distinguish "compartments" of body fat.

TABLE 4

Weight of subcutaneous adipose tissue as percentage of total body weight

GROUP	N	MEAN	RANGE
A	31	18.85	11.5–29.4
B	25	21.91	15.5–31.8
C	28	22.81	9.3–36.4

TABLE 5

Body fat compartments

GROUP	AGE	N	WEIGHT	TOTAL BODY FAT	SUBCUTANEOUS FAT	INNER FAT
			kg	*kg*	*kg*	*kg*
A	18–30	23	55.12	14.4	3.8	10.6
B	31–45	19	61.63	20.0	5.2	14.8
C	46–67	20	61.48	23.8	5.2	18.6

While the "total body fat" as estimated from specific gravity indicates a continued rise with age, the subcutaneous fat and total body weight do not increase from the middle to the oldest group. We must therefore conclude that the fattening of the female body during the later phase of maturity goes on principally by increasing the inner fat. Furthermore, since the total weight of the body is not changing, this accumulation of inner fat seems to be occurring at the expense of other tissues in the body. It is not yet certain how much of this increase may occur in fat depots and how much should be credited to a fatty infiltration of some organs. At any

rate, the deposition of internal fat may be an important component in the complex phenomenon of aging.

Regional changes in the distribution of subcutaneous adipose tissue with age apparently begin in both sexes early in childhood. Reynolds ('51) has found in school age children that the relative contribution of fat in the distal portions of the extremities to total subcutaneous fat declines. More and more of the subcutaneous adipose layer comes to lodge in the trunk and adjacent portions of the limbs, as measured from Reynolds' longitudinal series of soft tissue roentgenograms.

TABLE 6

Calculated thickness of a single layer of subcutaneous adipose tissue

AGE GROUP	MEAN THICKNESS, IN MM			PERCENTAGE DIFFERENCES		
	A	B	C	B vs A	C vs B	C vs A
Chin	3.5	4.0	4.6	14.3	15.0	31.4
Back	7.0	9.0	10.0	28.6	11.1	42.9
Chest	7.1	9.8	11.4	38.0	16.3	60.6
Side	5.7	8.5	9.2	49.1	8.2	61.4
Waist	7.0	9.4	9.5	34.3	1.1	35.7
Abdomen	12.5	13.6	16.0	8.8	17.6	28.0
Arm	9.9	11.4	12.2	15.2	7.0	23.2
Thigh	18.5	21.6	21.5	16.8	—0.5	16.2
Knee	6.9	7.8	7.5	13.0	—3.8	8.7
Calf	11.5	10.9	10.0	5.2	—8.3	—13.0

A cross-sectional sample of children from the Forsyth Dental Infirmary was measured with skinfold calipers by Baker. His unpublished data show the same pattern of redistribution in childhood. In table 6, comparable findings are presented for adult women.

It is evident that increases in subcutaneous adipose tissue with age are very much less striking in the extremities than on the trunk. With age, the largest relative increases are found in the flanks, chest and back. Lesser thickenings occur at the waist and abdomen, and in the chin region. In the lower extremities, some increases are seen proximally, but fat is apparently lost distally.

In table 7, the mean skinfold thicknesses of the female age groups are compared with data collected previously on men (Brožek, '52). It should be noted that in the male sample the average body weight was close to or identical with the 1912 medico-actuarial standards. The female samples, however, were systematically somewhat underweight.

In absolute terms, the age increments in the average values are almost identical (4.6 mm for men and 4.8 mm for women). Because of the higher initial female value, however, the ratio of mean skinfold thickness of older and younger subjects is

TABLE 7

Mean skinfold thicknesses in men and women, in mm

SEX	MEN		WOMEN		MEN		WOMEN		MEN	WOMEN
AGE RANGE	23–29		18–30		53–57		46–67		Increase in per cent	
MEAN AGE	25.2		24.0		54.6		55.4			
N	25		31		34		28			
	M	σ	M	σ	M	σ	M	σ		
Chin	8.9	1.9	9.1	2.5	11.0	2.7	11.3	3.5	23.6	24.2
Back	14.6	5.3	16.0	4.6	21.5	7.1	21.9	10.3	*46.8*	36.9
Chest	16.3	7.1	16.3	5.4	27.9	7.4	24.8	7.3	*71.1*	52.1
Waist	17.1	2.3	16.2	3.9	19.6	5.3	21.1	7.6	14.6	*30.3*
Abdomen	19.1	7.8	26.8	6.0	26.0	6.6	34.0	9.5	*36.2*	26.9
Arm	13.7	3.0	21.9	4.6	15.4	4.0	26.3	6.2	12.4	*20.1*
Knee	8.9	1.9	15.9	3.9	9.4	2.5	17.0	5.6	5.6	*8.3*
Mean	14.1		17.5		18.7		22.3		32.6	27.4

lower for women (1.27) than for men (1.33). The female/male ratio is 1.24 for the younger, and 1.19 for the older, subjects. These figures are not directly comparable with those of Edwards ('51), who considered the thickness of one layer of subcutaneous fat, free from the skin. Such an adjustment would automatically increase the female/male ratios to about 1.30 and 1.22, respectively.

In regional terms, table 7 indicates that in both sexes, the trunk gains more fat than do the limbs. Men acquire more fat in the back, chest and abdomen than do women. The female accretion of fat is more pronounced in the waist and arms.

In table 8, the data of table 6 are recast to show the relative percentage contribution of each skinfold site to the total thickness of the adipose layer in the female sample. The subcutaneous layer shows a relative increase in the trunk, especially on the side over the ribs and on the chest. While the panniculus adiposus of the abdomen shows absolute increases with age, its relative participation in the thickening of fat deposits over the entire body does not change consistently. The relative participation of the subcutaneous fat layers in

TABLE 8

Percentage contributions of regional subcutaneous fat deposits to the total thickness of subcutaneous adipose layer in the female series

SITE	A	B	C
Chin	4.0	3.8	4.2
Back	8.0	8.6	9.1
Chest	8.1	9.4	10.4
Side	4.2	6.2	6.6
Waist	8.0	9.0	8.6
Abdomen	14.3	13.1	14.6
Arm	11.3	11.0	11.1
Thigh	21.1	20.8	19.6
Knee	7.9	7.5	6.8
Calf	13.1	10.5	9.1
Percentage total	100.0	99.9	100.1
Total thickness (mm)	87.6	104.0	109.9

the extremities decreases, even though the arm, thigh, and even the knee gain in *absolute* thickness of the adipose layer.

Merging of some of the foregoing percentages provides still clearer evidence of age differences in female subcutaneous fat distribution. In table 9, comparisons are made of the upper versus lower regions, and of the axial regions of the body versus the limbs. The "upper" percentage is the sum of the arm, chin, back, chest, side, and half of the waist percentages. The "lower" is half of the waist percentage plus abdomen, thigh, knee and calf. The "axial" percentages are chin, back, chest, side, waist and abdomen. The "appendicu-

lar'' percentages are the sum of the arm, thigh, knee and calf percentages. The increase with age in the panniculus adiposus is present above the waist rather than below the waist, in the chin and trunk region rather than in the limbs. Age differences in the vectors of body form, as we shall see, closely parallel these metrical findings.

TABLE 9

Regional percentage contributions to total thickness of the subcutaneous adipose layer

GROUP	A	B	C
Upper body region	39.6	43.5	45.7
Lower body region	60.4	56.4	54.4
Axial	46.6	50.1	53.5
Appendicular	53.4	49.8	46.6

TABLE 10

Vectors present in the female series

VECTOR AGE GROUP	A	B	C
One-vector ''types''	55.7	52.0	40.7
Normal (N)	92.8	56.0	51.8
Rubens (R)	3.7	16.0	22.2
Superior (S)	3.7	8.0	3.7
Inferior (I)	25.9	28.0	18.5
Truncic (Tr)	0.0	20.0	14.8
Extremital (Ex)	7.4	4.0	7.4
Trochanteric (T)	11.1	12.0	25.9
Mammary (M)	3.7	8.0	18.5
Pseudosteatopygous (P)	0.0	0.0	3.7

Table 10 presents percentage frequencies of vectors observed in the female series. Since some individuals exhibit more than one vector, the sum of the percentages in each column of table 10 is greater than 100%. Several morphological trends are revealed by these percentages. Some confirm the evidence from the fat measurements while others yield

insights which could not be gained from the metrical data alone.

First of all, body "types" showing only one pronounced vector become less frequent with age. Evidently the amount of soft tissues in women becomes increasingly large and its distribution less harmonious. The frequency of N (and I) vectors decreases with age, whereas that of R, (Tr), T and M increases. In other words, the younger women tend to be more massive in the legs while in the older women the trunk gains soft tissue. The only woman with some pseudo-steatopygia (Pst) was found in the oldest group. In women over 46 years of age, fat deposits in the trochanteric regions and breasts also seem to be more conspicuous.

The skinfold measures and calculated thickness of subcutaneous fat, as shown in tables 6–9, provide quantitative evidence in partial support of the foregoing statements. Both methods stress the relatively rapid accumulation of fat on the trunk as opposed to the limbs, and the increase of the M vector shows that some of this accumulation is in the breasts. Furthermore, the quantitative increase of the panniculus adiposus above the waist illustrates the increasing importance of the S and Tr vectors, and the decreasing importance of the I vector. Some differences, however, are to be expected. "Subcutaneous adipose tissue" measured by skinfold calipers is not synonymous with visually estimated "soft tissues." Also, skinfolds were not measured in all sites critical for diagnosing the vectors. For example, one would have to measure a skinfold over the greater trochanter to characterize quantitatively the T vector. This, however, is a difficult site to measure because the skin is often tight.

DISCUSSION

Validity of the results

In some cases, the body form is conditioned more by muscle tissue than by fat. Thus, by inspection, 5 subjects appeared to have a well-defined I vector, but the leg showed a

subcutaneous adipose thickness below the mean. Here, the muscle tissue influenced the diagnosis. A somewhat similar situation was observed by Reynolds ('51, p. 152). A girl of 17 in his series showed a very pronounced bulge in the trochanteric region, but the roentgenogram indicated that the effect was due mainly to the formation of the trochanter, with a very much thinner adipose layer than might have been expected. If one does not insist on the definition of vectors in terms of "pure" adipose tissue, and is concerned with external body form rather than body build, it may be preferable to characterize the I vector, at least, on the basis of limb circumferences rather than from skinfolds alone. Škerlj ('38) has used such an approach. The T vector, and perhaps others too, may express underlying tissue as well as subcutaneous fat.

Measuring skinfolds — especially when combined with limb circumferences — permits a more exact discrimination between soft tissues than can be obtained from inspection. Such a discrimination is advantageous in diagnosing the nutritive state of the individual (Brožek, '53a). Skinfold measurements may be used to verify or correct inspectional ratings of vectors of body form. Such corrections have been made for the women studied here, but the material is not presented for lack of space.

Although the measurements used in the present study were not designed for the metric evaluation of body form, they appeared quite useful for characterizing at least some vectors. For this purpose, at least one measurement of the head and one of the forearm should be added. For a detailed description of subcutaneous adipose tissue, the following regions should be included: chin, neck, chest, back above the waist, abdomen, back below the waist, upper arm, forearm, thigh and calf. In calculating the "average" thickness of the subcutaneous adipose layer, some skinfolds should also be included where the fat is normally negligible or lacking: wrist, ankle, dorsum of the hand and foot, and perhaps the nose.

Future studies of age changes in human tissue distributions might well be planned better with respect to sampling. The subjects who volunteered for this study were actually drawn at random from our acquaintances. We talked to groups in the School of Public Health and Department of Home Economics of the University of Minnesota, and measured everyone who raised her hand.

In national origin, a somewhat larger representation of women of northwestern European ancestry was found in the older groups, and especially in the oldest. Angel ('49) states that women descended from northwestern Europeans show less obesity than those of central and southern European origin, and the same is true of over 40,000 Army men whose body build photographs were evaluated by Hooton ('48). Thus, as far as increases in fatness with age are concerned, the present data may be somewhat biased in the conservative direction.

Increases with age in circumferences of the body in women are well established, as shown in a sample of over 10,000 by O'Brien and Shelton ('41), and are presumably the results of fattening. Edwards ('50) minimizes the permanent effects of childbearing on this process, so that comparisons of younger and older women on the whole are probably not greatly affected by fluctuations in the number of pregnancies in the different age samples studied.

In calculating the amount of subcutaneous fat in the body from skinfolds, two sources of variation in the thickness of "skin" proper may be considered: the average differences between sites and inter-individual differences at the same site. No systematic data on the second question can be found in the literature. Edwards ('50) indicates that in women the thickness of two layers of skin varied from 1 to 4.5 mm at different sites, with a mean of 2.2 for 53 sites.

Also, there is the question of the compressibility of the skinfolds. The elastic properties of both skin and subcutaneous fat may vary in different parts of the body, to say noth-

ing of age and sex differences. Baker finds, in children, that boys' upper arm skinfolds differ in compressibility enough from those of the girls that male and female formulae have been calculated to translate skinfold thicknesses to roentgenometric depth.

Another source of possible error is the density of subcutaneous adipose tissue. We used the value 0.94, but we do not know whether this density is constant in both sexes, at all ages, or in all body regions. Densitometric evaluation of the fat content is a considerably more complicated matter than it has appeared (Keys and Brožek, '53). The calculation of total body fat from specific gravity is only an approximation, and the formula of Rathbun and Pace ('45) used in the present study is open to criticisms both on theoretical grounds and in reference to actual density values used for human fat and "fat-free weight." One of the basic assumptions is that the obtained density can be compared to the density of a reference body. However, bone becomes demineralized in old age, its density decreases, and the loss of bone minerals would influence the density of the body in the same direction as fattening. It seems unlikely, however, that this factor was important in the range of ages studied here. In starvation, furthermore, a loss of 25% in body weight was not associated with changes in bone density as measured from roentgenograms (Keys et al., '50). The facts remain that the subcutaneous fat layer becomes thicker with age — especially in the trunk — in both sexes, and in the proximal segments of the limbs in women and that the specific gravity of the body decreases with age. The estimation of the "inner fat" by the present technique is affected by errors in both components ("total" and "subcutaneous") and only the age trends, not the absolute values, can be taken seriously. The adipose tissue contains about 42% of chemically extractable fat (Mitchell et al., '45) but this percentage may show considerable individual variations.

Comparisons with data in the literature

Comparing the age changes, indicated by inspection and by skinfold measurements in women, with the trends observed in men (Brožek, '52) we find that in both sexes the trunk gains a good deal of adipose tissue, the men's gain being considerably greater. This results in an increasing typological similarity of the sexes in late middle age. In men one often sees at this time a development of the M vector. Apparent sex differences are preserved in the limbs, at least in their proximal segments.

An unpublished study of age changes in body form in men has also been carried out at the Laboratory of Physiological Hygiene, University of Minnesota. A sample of more than 100 young men of college age, and about 300 middle aged men were examined. Anticipating the results of this study, we see the same characteristic differences in the percentage of form types: the Ex and I vectors are typical of young men, and the S and Tr vectors for the middle aged, as was true of the much smaller sample of women.

Some comparisons are also possible with Reynolds' data ('48, '49) on the tissue composition of the leg at the level of the greatest calf breadth. While sex differences are brought out clearly in the absolute breadths of the lateral plus medial "fat" tissue (9.6 mm for men, and 19.7 mm for women), the differentiation becomes still more marked when the breadth of bone is used as the reference point, with mean values of 28 and 61, respectively, for the fat/bone index.

In normal women, Angel ('49) gives a fat + skin value of 10.4 mm, as measured at an unspecified site from roentgenograms of the chest. In the Minnesota study, Group B (the women aged from 30 to 45 years) had an average of 10.8 on the chest, and 9.5 on the side over the ribs. As Angel's series were about the same age, these estimates seem comparable.

Interesting age trends in body form may be noted in Edwards' table 3 ('51). While in pubertal girls the subcutane-

ous fat thickness measurements above the waist contributed 55% to the total, in nulliparous and parous women this value increased to about 57%, and to 60% in menopausal women. A similar trend (41, 44, 47%, respectively) is present in the axial measurements. Although the sites included in Edwards' and our series were different, Edwards' data indicate the same trend as seen in our table 9.

Finally, the age trends in adult female body circumferences found by O'Brien and Shelton ('41) indicate that gains are more rapid before the age of 40 years than later. This is particularly true for the girths of the abdomen and of the waist. On the other hand, the circumferences of mid-thigh and upper arm increase only slowly. The percentage participation of these limb circumferences in total circumferential gain steadily decreases. The trend toward increases in girths of the trunk relative to those in the limbs is quite clear from this material.

CONCLUSIONS AND UNANSWERED QUESTIONS

The following conclusions can be drawn from the material presented here.

1. The human body tends to increase in fatness during aging in both sexes.

2. This fattening takes place more in the trunk (both in subcutaneous and inner fat) than in the extremities. Thus, the humorous definition of adulthood as "the age when all growth stops except in the middle" has a realistic basis.

3. Weight changes during aging represent a complex phenomenon, involving simultaneous changes in several tissues and a redistribution of the subcutaneous fat.

4. The relationship of total body fat to subcutaneous fat may be a useful measure of the aging process.

5. The numerous sources of error indicated for the present measurements make them quantitatively inaccurate, and much more suitable for indicating group trends than for describing single individuals. We believe, however, that the major findings in this study are unequivocal.

6. At the same time, important methodological and theoretical questions have been raised which can only be clarified by further research and more precise measurements.

In reducing, is the subcutaneous fat the first reserve which is diminished, and is the pattern of depletion the same at all ages and in both sexes? Furthermore, does weight reduction differ in the various kinds of obese body forms? For example, does an Ex form lose fat first in the extremities and not in the abdomen or somewhere else in the body? Does the Tr form show an opposite tendency? In reducing, do the vectors reflecting more localized depots of subcutaneous fat decrease, and does the body form approach the normal (N)? Edwards' results ('50, '51a) suggest that the answers to most of these questions would likely be negative. For men, changes of body build in starvation were described by Lasker ('47) and by Brožek and Keys ('52).

There is a large practical problem of controlling the insidious onset of obesity in many individuals (Brožek, '53b). Although the fattening process is clearly a matter of "overeating," there are wide variations in what constitutes a caloric excess for different individuals. This variability probably arises chiefly from different amounts of physical activity (Hunt, Peckos and Fry, '53). The question still remains: what can be done to modify metabolic or hormonal processes which control the deposition of fat in restricted areas of the body (Edwards, '51a)?

SUMMARY

In the summer of 1952, 84 "normal" women were examined at the Labratory of Physiological Hygiene, University of Minnesota. The overall study was designed to evaluate changes in body composition, with special reference to the fat content, and paralleled similar work on men (Brožek, '52). Skinfold thickness was measured at 10 sites with spring calipers and the fat content of the body was estimated from specific gravity. The body form of these women was appraised by inspection.

Three age groups were studied (18–30, 31–45, and 46–67 years). Pronounced age differences in the amount and distribution of soft tissues were noted. The "normally" proportioned body forms, with moderate amounts of fat harmoniously distributed, became less frequent in the older groups while harmoniously obese forms increased. Physiques showing an abundance of soft tissue in the extremities and lower parts of the body decreased in the older groups, while women with considerable fat on the trunk, breasts, upper arms, chest, and trochanters increased.

Although the patterns of subcutaneous fat distribution changed, and in most instances showed an overall increase, the "inner fat" seemed to increase more than the amount of the subcutaneous fat. Perhaps the rate of accumulation of inner fat — a phenomenon quite inaccessible to traditional anthropometry — will prove to be a useful criterion of aging in future nutritional and constitutional investigations.

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REVIEWS

SWARTKRANS APE-MAN, PARANTHROPUS CRASSIDENS. By Robert Broom and J. T. Robinson. Transvaal Museum Mem. No. 6. xii + 123 pp. Transvaal Museum, Pretoria, South Africa.

This is the third volume of a series describing the morphology of the South African australopithecine man-apes. The Swartkrans deposits were worked in 1948–49, and along with the earlier known sites of Sterkfontein and Kromdraai, are situated in a shallow valley some 6–7 miles northwest of Krugersdrop in the Transvaal. The man-ape fossils occur in breccia deposits of calcite-cemented sand accumulated within dolomitic limestone fissures.

The *P. crassidens* skeletal material described here comprises for the most part broken and crushed skulls and jaws. The series includes 5 lower jaws (juvenile and adult), another mandible with the adjoining mid-facial region, two fairly complete but crushed adult crania, and two crushed juvenile crania. A fairly complete right innominate and the inferior half of a humerus (not described) are also referred to this species. Brief chapters are devoted to the main features of these specimens by Broom and more extensive treatment of the permanent dentition by Robinson.

Another type occurs in the deposit and is referred to *Telanthropus capensis*. It is known from a nearly complete mandible with teeth and a portion of radius (undescribed). More recently, a portion of the snout of *Telanthropus* has been recovered and briefly described (Robinson — Nature, *171:* 33. 1953). Since this mandible was found in a patch of somewhat darker matrix than that containing *P. crassidens*, this fact as well as the more hominid anatomy suggested a different age for the specimen. Robinson (Ann. Trans. Mus., *22:* 1–19. 1952) has recently stated, however, that a fluorine test made by K. P. Oakley has indicated "no significant difference in the fluorine content of this and *Paranthropus crassidens* specimens," indicating that "there can be no major age difference between them — if the fluorine test is valid for specimens fossilized under these South African conditions." An additional fragment of horizontal mandibular ramus is also regarded as another hominid type, probably distinct from *Telanthropus*.

The innominate bone was found isolated (with the humerus fragment) but near fragments of three skulls of *P. crassidens* so that

Broom and Robinson feel justified in regarding it as belonging to this form. The discovery of this piece casts important light on the locomotor mechanism of this animal. The bone is in many respects hominid although it differs from the modern human condition in several significant respects. The blade of the ilium is broad and non-anthropoid in conformation. The iliac crest is not preserved but its form can be reasonably reconstructed. It is hominid in contour but less curved and wider than in man. This crest is more posteriorly situated than in man and indicates perhaps a difference in manner of weight-bearing. The sacral articulation is larger than that of modern Bushmen or *Plesianthropus,* the latter having a smaller articulation than man. The anterior superior iliac spine is considerably more developed than in *Plesianthropus* or in man. The anterior inferior spine is better developed than in *Plesianthropus* and the relation of the base of the spine to the acetabulum is more hominid than in *Plesianthropus.* The acetabulum is hominid in conformation although smaller than in man. The superior portion of the pubis is considerably thickened anterior to the acetabular margin and heavier than in most men.

The ischium is peculiar and distinctive in all of the man-apes where known and can be labelled neither hominid nor anthropoid. In *P. crassidens,* the broad, extensive ischial tuberosity of man is absent and there is instead a short, flange-like process; there is thus a wide groove between the upper margin of this process and the rim of the acetabulum. The ramus of the ischium is a long and robust process, more powerfully developed than in man and also unlike the slender ramus of *Plesianthropus* (this may well be a sexual difference, however, *P. crassidens* probably male, *Plesianthropus* probably female, from the character of the sciatic notch).

As Broom notes, both the *Plesianthropus* and the *P. crassidens* innominate bones are less hominid than the adolescent fragment from Makapansgat ascribed by Dart to *Australopithecus prometheus.* Nevertheless, neither are anthropoid and the morphological evidence indicates that these forms must have walked upright although the differences in the ischial region and the anterior iliac spines suggest that bipedal progression was not the same or as fully developed as in man. These bones merit careful comparative study in the future with a view towards determining more precisely the nature of man-ape locomotor habits.

The cranial morphology of *P. crassidens* is still incompletely known, not because of lack of material but due to the crushed nature of the recovered specimens and the lack of manpower to clean and prepare the material. Broom's description and illustration provides, however,

a good outline of the main features. He estimates cranial capacity at 800–850 cm^3 for females and 1000 cm^3 or more for males, but this estimate may be excessive. A striking feature of the vault is the presence of a marked mid-sagittal crest. The parieto-squamous suture is long and low, and in at least some specimens there is an alisphenoid-parietal junction at pterion. The cranial base is preserved but as yet inadequately cleared. In the adult, there is a deep glenoid fossa, large rounded external auditory meatus, well-developed mastoid processes, and an occipital torus, the form of which is not given by Broom. The base is best preserved in the two juvenile skulls in which one notes hominid occipital condyles, a large and flat nuchal area, and an anterior situation of the foramen magnum.

The adult face is considerably well preserved. There is a robust suprafacial torus, most marked at glabella and thinning out laterally but still heavy. Above glabella, the brow region is concave due to the supero-medial extension of the anterior portion of the temporal line superiorly to the sagittal crest; there is also marked postorbital constriction. The nasal bones are fairly long and in at least one specimen fused. The orbits appear fairly small and square; the interorbital distance is considerable. The nasal aperture is short and broad. The maxillary region is flat below the orbits although there is some hollowing above the molar region. The malars are prominent and flaring and the masseter muscles must have been powerful. Where preserved, the zygomatic process is deep and heavy. There are marked canine pillars extending upward along the margins of the nasal aperture. The supra-incisive area is hollowed out so that there is considerable guttering back into the nasal aperture where there is a rudimentary nasal spine. The palate is a broad ∩ or ⊓ shape with a deep incisive fossa. The mandible is extremely thick and massive bone with a high and fairly wide ascending ramus. The coronoid process is high and posteriorly curving, and the thick bone below it, along with the sagittal crest and high ascending ramus of the mandible, suggest extremely powerful temporal muscles. The mandibular symphysis is heavy and thick inferiorly but the alveolar region is much thinner. In several specimens, there is an indication of a slight mental prominence but in other specimens this area is gently curved and no "chin" is present.

The dentition is very well known and has been well described. The sequence of eruption of the permanent teeth differs from that of the anthropoids in that C and P1 erupt before M2, P2 erupting after M2 and before M3. This sequence differs from that of modern men in which the two premolars and the canines erupt before the second molar. The upper deciduous dentition is poorly known but the lower

is known completely. The incisors and canines are small (the latter being bi-cuspid), the milk molars definitely hominid — the first with 4 cusps and well developed anterior fovea, the broad square second milk molar with 5 main cusps and one smaller cusp.

The permanent dentition is known from more than 200 teeth and Robinson has offered an excellent description of this set based on 116 upper and 82 lower specimens. The anterior teeth, canines and incisors, are strikingly small compared to the large premolars and molars. The upper incisors are shovel-shaped. The 4-cuspid upper molars, which are clearly hominid, show traces of Carabelli's cusps, pits, and grooves; these teeth increase in size from *M1* to *M3*. The lower dentition is typically hominid in pattern although in size outside the range of human variability. The lower first molar frequently bears a tuberculum sextum. The wear of the teeth is smooth and regular and clearly hominid, not like the uneven wear of the anthropoids. Robinson gives a description of these teeth as well as some comparative observations with the other man-apes and *Pithecanthropus* and *Sinanthropus*.

On the basis of differences in morphology (a lower ascending ramus, less robust structure, smaller teeth, differences in dental morphology) Broom and Robinson regard the *Telanthropus* specimen as true "Homo" and perhaps a descendant of the australopithecine group. They regard the man-apes "as being more or less terminal twigs" of a group "the maximum development" of which "probably occurred during the Miocene and Pliocene and survived a short way into the Pleistocene." "During this period at least one of the australopithecines, possibly more than one and possibly not only in Africa, rapidly evolved into a true hominid. The descendants of this type — or these types — have since provided the human population of the world."

Robinson (this journal, *11:* 1–38. 1953) has recently shown the resemblance of "*Meganthropus africanus*," found by the Kohl-Larsen expedition near Lake Eyasi, Tanganyika in 1939, to the man-apes, especially *Plesianthropus*. This suggests that the man-apes will be found in other areas of Africa to the north of the type area. He has also noted the similarity of the *Meganthropus palaeojavanicus* jaw fragment from Java to *P. crassidens* and suggested a relationship between these forms; this is a fact difficult to dispute since the likeness is quite striking. The man-apes would thus appear to have been widespread over a considerable area of the Old World, and Robinson suggests that some members of this group were ancestral to true men ("euhominids" of Heberer). On the basis of the present evidence, the reviewer is inclined to agree with Robinson's conclusions and can

see no objections, since some of the man-apes are most probably Villafranchian in date, to include at least some of these animals in human ancestry.

This volume is a fitting memorial to Doctor Broom who devoted the final years of his life to accumulating evidence on one of the major phases of human evolution — the beginning of bipedalism. That his work confirms the earlier views of Dart few can now justly question. One cannot but be impressed by not only the number of remains collected from the Sterkfontein — Kromdraai — Swartkrans sites but also the importance which these fossils have for any conception of human evolution. Certainly an animal which had assumed bipedalism, however imperfect, and which carried a hominid dentition in a cranium with curious mixtures of "anthropoid" and "hominid" characters should fulfill any conception of a "missing link." Yet the controversy which has been aroused over the discoveries has yet to die down and a sound appraisal of their true character yet to be made by many workers outside of Africa. This report by Broom and Robinson should go a long way to convince some of the sceptics who doubt the essentially hominid nature of the material. These fossils are among the most important discoveries ever made in human paleontology and they deserve the most careful study and evaluation. The richness of the deposits from which the man-apes have been recovered hint at what we may expect in the future from this area of the world. One can only hope that future findings will be received more dispassionately than those of the past.

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EVOLUTION IN ACTION. By Julian Huxley. x + 182 pp. Harper & Brothers, New York. 1953. $2.75.

Dr. Julian Huxley is the most prolific contemporary biological writer. Twenty-seven books of which he is the author or a co-author are listed facing the title page, and this reviewer notices that at least one book has been overlooked. Of course, this list does not include the numerous discussion articles and research papers which Doctor Huxley has published, or the writings incidental to his tenure of the post of Secretary General of UNESCO. One book characteristically entitled "Religion without Revelation" stands as a watershed in Doctor Huxley's long writing career. A master of fluent and informative presentation of biological subjects emerges as a philosopher who attempts no less than to build a new religion, for which he suggests

the name of "Evolutionary Humanism." One cannot help thinking at this point about the quite independent, and yet in so many ways parallel, career of Doctor Huxley's equally famous brother, Aldous Huxley.

The focus of the short but pithy book under review is clearly in its last chapter, on "The human phase" (of evolution). Here the essence of the book is stated thus: "Medieval theology urged men to think of human life in the light of eternity — *sub species aeternitatis:* I am attempting to rethink it *sub specie evolutionis* — in the light of evolution." The result is the evolutionary humanism, which "is capable of becoming the germ of a new religion, not necessarily supplanting existing religions but supplementing them." With due apologies to the author of "Religion without Revelation," the following statement may be regarded the basic revelation of the new religion: "In the light of evolutionary biology man can now see himself as the sole agent of further evolutionary advance on this planet, and one of the few possible instruments of progress in the universe at large. He finds himself in the unexpected position of business manager for the cosmic process of evolution." From this premise follow criteria for "scientific" morality and ethics: "anything which permits or promotes open development is right, anything which restricts or frustrates development is wrong. It is a morality of evolutionary direction." The limitations of these criteria from the evolutionary viewpoint have been discussed in recent years by several authors — suffice it to name only G. G. Simpson in the "Meaning of Evolution" and C. D. Leake and P. Romanell in "Can we agree?" It is, however, understandable that Doctor Huxley is concerned in this little book with stating his beliefs and not their possible limitations.

To an evolutionary humanist, the importance of the science of life and the science of man cannot be overestimated. Indeed, "In this light the highest and most sacred duty of man is seen as the proper utilization of the untapped resources of human beings." But "the human sciences today are somewhat in the position occupied by the biological sciences in the early 1800's; they are rapidly exploring different sectors of their field, but still looking for a central core of general principles." This central core will be found when matters are considered "*sub specie evolutionis.*"

The first 5 chapters of the book are clearly ancilliary to the climax of "The human phase" in the 6th chapter. It would be very difficult in a brief review even to enumerate the topics dealt with in these ancilliary chapters, and the chapter headings give only inadequate descriptions of their contents. In them, Doctor Huxley ranges over general biology, zoology, botany, embryology, genetics, paleontology, physiology, psychology, and physical and cultural anthropology.

Thanks to his remarkable skill as a writer, he manages often to put in a paragraph a great deal of information as well as an interpretation. Specialists in the respective sciences will probably find more or less numerous points on which to disagree with the author or to wish that his statements were less dogmatic. But such disagreements may appear to be puny quibblings when one remembers that this book aspires not just to describe scientific findings but to build a scientific religion.

To say that this is a thought-provoking book would be an understatement: it is, to a biologist or an anthropologist, one of the most thought-provoking books ever written. It can hardly be recommended as a source of information, although it mentions a very wide variety of information. But it can be recommended very highly as a source of inspiration, for it shows that the everyday drudgery of scientific research may yet lead to understanding of the "overall relation between man and his destiny."

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FOOD FOR LIFE. R. W. Gerard, Editor. University of Chicago Press. 1952.—This well written and edited authoritative book on nutrition is designed to give the public sound and up-to-date information on the subject. It accomplishes its stated purpose easily, yet this is not what distinguishes this book. Rather it is the interest in the evolution of nutritional adaptations and comparative physiology seen in this light that makes it exceptional. Too rarely the books on nutrition see their subject from a broad biological viewpoint, and almost never is nutrition seen as an adaptational system where organism and environment meet. Although not couched in the professional's terms, this book is not lacking in ideas or depth and is distinguished by its breadth. This breadth is obtained by variety in subject matter, viewpoint and from a generous leavening with data.

HUMAN ENGINEERING.— Edited by Lawrence Edwin Abt. Annals of the New York Academy of Sciences. Vol. 51, Art. 7, pages 1123–1278, New York. 1951.

"Human engineering" is a term that sounds so impressive that anthropologists, psychologists, and social workers have all used it to emblazon their banners. In the present volume, the term human engineering is used in a relatively unobjectionable way. Human engineering is considered to be the application of psychometric or anthropometric data to practical problems involving comfort, reaction time, size, motion and the like.

Many of the papers contained in this volume are of primary interest to those physical anthropologists engaged in "applied anthropometry." A few, however, that have to do with size, motion, and fitness are of general interest. The papers by Catranis, Elftman, and Taylor and Blaschke are especially welcome, since the official reports on their work have not been generally available in the past.

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